THE UNIVERSITY OF ALBERTA

GENETIC VARIABILITY OF WHITE SPRUCE (*Picea glauca* (Moench) Voss) in ALBERTA

by

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A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

IN

FOREST SCIENCE

DEPARTMENT OF FOREST SCIENCE

EDMONTON, ALBERTA

FALL, 1977

ABSTRACT

Twenty seven sources of white spruce (*Picea glauca* (Moench) Voss) were used to investigate the nature and amount of genetic variability of white spruce in Alberta. These sources were grown in containers for two growing seasons, in a factorial design, under two controlled environment regimes simulating northern and southern Alberta forest conditions. Of 12 characters measured, only total and top relative dry matter and number of branches were found to have significant among-source variation. Northern Alberta sources had significantly higher total and top relative dry matter than all other sources tested in both environments. Sources from central and north-central Alberta had significantly more branches than all other sources tested.

Relative dry matter increased continuously with latitude and elevation of the source. Number of branches exhibited a banded pattern of variation. It is possible that the patterns of variability illustrated in this study could have developed from the retreat and reestablishment of white spruce in north and north-central Alberta during the late post-glacial period.

ACKNOWLEDGEMENTS

I would like to express my appreciation to the Alberta Forest Development Research Trust Fund for their financial assistance throughout this project. I would also like to thank the Alberta Forest Service for the use of their white spruce seed and seed source information. The staff of the Department of Forest Science extended me considerable assistance throughout the project and I would like to extend my gratitude to them. Finally and most importantly I would like to thank Dr. B. P. Dancik without whose encouragement, assistance and friendship this thesis would not have been possible.

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I. Introduction

Background to the Problem

White spruce [*Picea glauca* (Moench) Voss],[1] one of the most widely distributed conifers in North America, grows naturally throughout the transcontinental boreal forest of Canada and the northern United States (Fig. 1). Altitudinally it reaches from sea level to 5000 feet. This species grows on a variety of soils ranging from heavy clays to alluvium and under a variety of climatic conditions ranging from wet to semi-arid (Nienstaedt 1957, Nienstaedt and Teich,1972). The major use of *P. glauca* is for pulp, but it is also used for timber, veneer and specialty woods (ie. oars and paddles).

Over the past twenty five years, the demand for and subsequent use of the white spruce resource has increased. Available land for timber production has gradually diminished over this time period (Anonymous 1947, 1971b). These trends may continue to at least 1990 (Manning and Grinell 1971, Jones 1975). In the past, increasing productivity through silvicultural treatments has been a satisfactory means of meeting increases in demand. However, the time is quickly approaching when it will become economically desireable not only to improve the environment

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[1] The authority for all Latin names used in this text is Hosie (1969).

Figure 1. Geographic distribution of white spruce in North America (Nienstaedt and Teich 1972).

in which stands are grown, but also to plant and harvest genetically improved stands of white spruce.

Wide-ranging forest tree species such as *P. glauca* have differentiated and adapted to many different sites (Roche, Holst and Teich 1969, Callaham 1964). This differentiation leads to a high degree of variability within the species. It is this genetic variability that has yet to be fully realized and utilized by users of white spruce. Before any plant species can be genetically improved one must have some idea of the degree and pattern of variability that exists in its wild populations. To do this one must undertake studies of variation within the species. These studies, whether biosystematic, genecological, provenance or seed-source studies, will help elucidate:

1. the degree of genetic variability within the species,
2. the pattern of inherent variability with respect to environmental variation,
3. the critical environmental factors, if any, that have acted to shape the observed pattern of variability (Callaham 1964).

Review of Literature

Provenance research, the "comparitive culture, under similar external conditions of plant material originating from geographically or environmentally different sites." (Langlet 1971), has made up the majority of the literature

on variability in _P. glauca_. Nienstaedt (1968) studied growth characterisitics of sixteen white spruce seed sources planted at fcurteen locations. Plants from Labrador, Alaska, Saskatchewan and other northern areas were found to grow more slowly than those from the Lake States, Quebec and Ontario. Nienstaedt suggested that the species may be exhibiting two clines of variation. One extends from the Lake States-Ontario region northwestward to Alaska. The second cline extends from the same area northeastward into Labrador.

Wilkinson et al. (1971) carried out a chemosystematic study on plants of the same seed sources. The pattern of monoterpene variation of the sixteen sources was analyzed in a plantation in southern Michigan. It was hoped that monoterpenes would give a better evaluation of genetic variation than growth or morphological characters. The monoterpenes indicated two clines of variation with a pattern similar to that shown in the Nienstaedt (1968) study. This confirmed that there is a clinal pattern of variation in white spruce.

A third significant study of _P. glauca_ genetic variation was carried out by Miksche (1968). Miksche found that the variation in amount of DNA per cell in root-tips of seedlings from seventeen sources was proportional to nuclear size. There were two distinct groups of sources, an eastern and western group with a division along the 95th Meridian.

DNA content per cell increased as latitude increased in the western group, but there was no significant trend within the eastern group. Significant differences in growth were noted between two-year old seedlings of the two groups. In the western group growth response significantly decreased with increasing DNA content per cell. In the eastern group no significant trends existed.

From these studies there appears to be a clinal pattern of genetic variation in white spruce related to latitude. Furthermore, two clines appear to exist. The first stretches from the southern Great Lakes region northwestward to Alaska, the second from the same area northeastward to Labrador (Fig.2).

On a more local and intensive scale some studies of variation within P. glauca have been carried out in British Columbia, Ontario, Newfoundland and Alberta. In British Columbia Roche (1969) initiated a genecological study of the growth of spruce sources under uniform environmental conditions and the cone morphology of field populations. In both cases clinal variation paralleled differences in elevation. It was hypothesized that photoperiod and its interaction with temperature were the most influential environmental parameters shaping this pattern of variation.

Teich and Holst (1974) found that Ontario white spruce provenances from limestone sites were ten per cent taller than provenances from granitic sites when grown on limestone

Figure 2. The two clines of variation in white spruce related to latitude.

sites. This trend was reversed on granitic sites. In another Ontario study Teich, Skeates and Morgenstern (1975) tested provenance height growth of Ontario sources on several sites throughout the province. After thirteen to twenty years, local provenances performed near the mean, but the best performance (twenty-one per cent taller) was from sources from eastern and southeastern Ontario.

In Newfoundland Khalil (1974) found that of a number of Great Lakes - St. Lawrence region provenances, eight from the southeast portion of the Quebec - Ontario border area showed the best height growth after fifteen years in a Newfoundland plantation. Results also indicated that a strong correlation existed between seven and fifteen year heights as well as a significant relationship between fifteen year height and latitude, longitude, mean January minimum temperature, and mean number of frost free days of the provenance.

The majority of variation studies of white spruce in Alberta have been taxonomic or chemosystematic in nature, and give some indication of local variability within *P. glauca*. Horton (1959) looked at cone scale morphology of white and Engelmann spruce (*Picea engelmannii* Parry) on three different site types in Alberta. White spruce predominated in valleys below 5000 feet and Engelmann spruce above 6000 feet. Between 5000 and 6000 feet a complex gradient or "hybrid swarm" existed that developed from

introgressive hybridization between the two species (Horton 1959). Taylor (1959) looked at a random collection of cone scales and needles of Engelmann and white spruce in the Banff - Cranbrook region of British Columbia and Alberta. While cone scales could be used to distinguish between the two, the differences were not great enough to warrant specific status. Instead, he suggested they were subspecies, with the intermediates expressing the variability between the two. Hellum (1968) found no correlation between cotyledon number or seed weight and latitude, longitude or elevation of forty sources from a number of forest regions in Alberta. However, significant differences were noted between broad forest regions with respect to seed weight. Seed from the foothills region (particularly the Kananaskis - Bow area) was heavier than seed from elsewhere in the province. Hellum indicated that these differences were due to genetic mixing of foothills sources with higher elevation Engelmann spruce, which have characteristically heavier seed. Monoterpenes and cone scales of white and Engelmann spruce sources along the Bow River in Alberta indicated that four spruce types could be delimited (Ogilvie and Von Rudloff 1968). These types described the gradient from "pure" white spruce to "pure" Engelmann spruce with introgressive hybrids between these two extremes. In another study in the same area differences in needle extract composition as well as morphology were not significant between P. glauca and P. engelmannii (Laroi and Dugle 1968).

The authors suggested that although white and Engelmann spruce have differentiated over most of their respective ranges, their data provided no evidence of common ancestry or for considering the two as subspecies; instead, they should be maintained as separate species. Hellum (1971) investigated seed weight distribution of white spruce from one hundred-sixteen sources distributed throughout Alberta. Correlation analysis indicated that no significant trends existed between source seed weight and any of several environmental parameters. However, certain groups of sources were significantly different. Seed from a central zone (53-57°N) was found to be significantly lighter than seed from either the northern (57-60°N) or the southern (49-53°N) zone. Daubenmire (1974) studied needle and cone morphology of *P. glauca* and *P. engelmannii* within and outside of their area of sympatry and found that *P. engelmannii* and *P. glauca* could be distinguished outside of the area of sympatry. Within the area of sympatry, however, morphological characteristics appeared to have "fused completely." Evidence of introgression existed within the area of sympatry with the "downward movement of *P. engelmannii* genes being more pronounced than the upward movement of *P. glauca* genes."

Study Objectives

It is evident from the preceding review that there exists a great deal of genetic variability within *P. glauca*.

This variability appears to be continuous in nature. The same degree of variability may exist on a more localized scale in Alberta. However, no properly designed genecological, biosystematic or provenance study has been undertaken to determine the actual degree or pattern of genetic variability and the critical environmental factors which affect the variability of *P. glauca* in Alberta. Thus this study will attempt to determine:

1. the amount of genetic variability within *P. glauca* in Alberta,
2. the pattern of genetic variability within *P. glauca* in Alberta with respect to environmental variation,
3. the critical environmental parameters, if any, which have acted to shape the observed pattern of variability,
4. the degree to which seed sources may be successfully transferred within Alberta,
5. if any of the chosen sources perform exceptionally well under environments differing from their local environments,
6. if there exists sufficient genetic variability to warrant the establishment of seed collection and planting zones for white spruce in Alberta.

II. Experimental Design

Null Hypotheses and Introduction

In this study the null hypotheses are:

1. that there are no statistically significant differences among Alberta seed sources of white spruce, grown in a common environment, with respect to any measured characteristic,
2. if significant differences do exist, they are not genetic in nature,
3. if significant differences do exist, they exhibit no discernible trends or patterns with respect to several environmental parameters.

To adequately design an experiment to investigate genetic variability within a species one must have an understanding of how the genetic component is interrelated with the measurable character or phenotype. Levine (1968) stated that "the expression of the phenotype is attributable not only to the genotype but to environmental conditions as well .... The environment therefore provides the arena in which the genotype acts; and accordingly the phenotype represents the ultimate expressions of the interaction of the genotype and its environment." This may be more simply expressed as:

$$P = f(G,E)$$

where, P= phenotype

G= genotype

E= environment

Allard (1960) stated that "In describing the phenotype it is convenient to express the joint action (of genotype and environment) in a linear fashion ...." Thus $P= f(G,E)$ becomes:

$$P= G+E$$

This is the case for the individual. However, in looking at species diversity one must be concerned with populations rather than specific individuals. Phenotypic expression of a given character within a given population can be described by its mean and standard deviation. This "variousness" or "existing condition of being various" (Langlet 1971) arises from the interaction of "envircnmental influences" and "hereditary endowment" (Philiptschenko 1927 in Dobzhansky 1970). It follows that variation in phenotypic expression within a given population may be more conveniently expressed as:

$$V_p= V_g+V_e$$

where, V= variance g= genotype

p= phenotype e= environment

Examination cf this relationship reveals that, if environmental variation can be held constant, one can say with some certainty that variation in phenotypic expression is primarily due to genetic constitution.

Study Design

In the present study controlled environment chambers were employed to minimize environmental variation. Twenty-seven sources of white spruce seed selected from the Alberta Forest Service seed bank (Fig.3, Table 1) were planted in a factorial design in each of two growth chambers and grown for two simulated growing seasons. The factorial design of this experiment consisted of two environments (i. e. treatments) with three replicates per environment. The 27 sources tested were randomized within each replicate. Analyses were carried out using replicate means for a given character (based on from one to six individuals). Missing values were accounted for in the analysis of variance using a weighted average approach (i. e. classical approach option under SPSS subprogram ANOVA; Nie et al. 1975). The seed sources were selected such that altitudinal and latitudinal gradients could be analyzed. Thus, three groups of sources were used to analyze elevational gradients along the east slope of the Rocky Mountains. Each group contained three sources representing high, intermediate and low elevation sites. The latitudinal gradients consisted of an eastern and western transect. The eastern transect (eight sources) extended from the southern boundary of the green zone in the St. Paul - Athabasca region to Ft. Smith in the northeast corner of the province. The western transect (nineteen sources) extended from the United States border along the east slope of the Rocky mountains (east slope sources) north

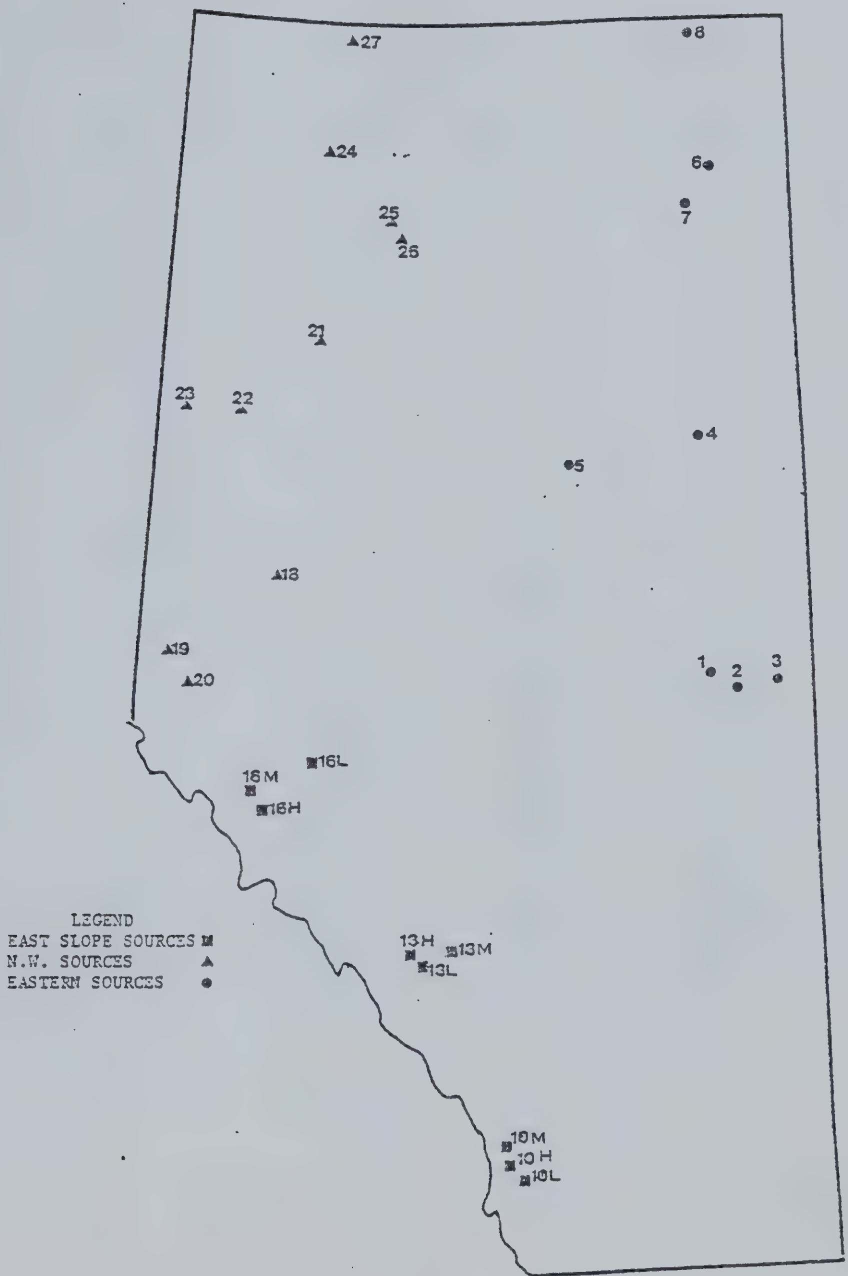

Figure 3. The 27 white spruce sources used in this study.

Table 1

SOURCE	LAT. (°N)	LONG. (°W)	ELEV. (M.)	CLAT.[2] (°N)
1	54.6	112.5	610	54.6
2	54.5	111.0	460	52.3
3	54.4	110.6	520	53.5
4	56.6	111.2	460	55.1
5	56.3	113.0	760	57.8
6	58.8	111.3	240	55.2
7	58.3	111.6	210	54.4
8	59.8	111.7	180	55.6
10M	49.8	114.6	1370	57.4
10H	50.2	114.5	1680	60.8
10L	49.7	114.5	1220	55.8
13L	51.8	114.9	980	55.4
13M	51.8	114.7	1220	57.9
13H	51.8	115.1	1370	59.4
16L	53.6	116.3	880	56.3
16M	53.5	117.5	1160	58.9
16H	53.3	117.5	1520	62.4
18	55.3	117.8	670	55.9
19	54.8	119.3	760	56.3
20	54.5	118.6	910	57.5
21	57.2	117.5	470	55.8
22	56.5	118.7	670	57.1
23	56.6	119.6	760	58.1
24	58.7	117.2	460	57.2
25	58.0	116.5	260	54.7
26	57.9	116.4	760	59.4
27	59.7	117.2	300	56.6

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[2] CLAT.=((ELEV.-606.1)/100)+LAT. (Wiersma 1964).

through the Grande Prairie area to the northwest corner of the province (Fig.3).

The twenty seven sources were grown in Spencer - Lamaire six packs throughout the study period. These containers consist of plastic compartments (six to a package) which, when in tray-form (seventeen packages per tray), were easily packed with soil medium (pure peat) and planted. Regular watering, approximately twice a week, began four weeks after seeding. The seedlings also were fertilized bi-weekly with nutrient solution (approximately 1 liter per tray of 112 p.p.m. N, 69 p.p.m. P, 156 p.p.m. K). Six weeks before the end of each growing season, regular waterings were reduced to once a week or whatever was just sufficient to keep the seedlings from wilting. At this time, a hardening-off solution of 32.87g of 10-52-10 in 40 liters of water was used bi-weekly in place of the regular nutrient solution until the end of the growing season.

As indicated previously growth chambers were used in this study to simulate two growing seasons. These chambers had the capability of controlling light intensity, photoperiod, day-night temperature and relative humidity (Appendix A). The two growing seasons used as test treatments simulated northern and southern Alberta spruce forest growing seasons (Appendix B). Simulation conditions were based on data from Ft. Smith, N.W.T., and Pincher Creek, Alberta, meteorological stations (Anonymous 1971a,

Anonymous 1968, List 1966).

Measurements and Analysis

During both growing seasons individual height measurements were carried out bi-weekly. Between growing seasons the seedlings in each environment were subjected to ten weeks of 4°C day-night temperatures (with some supplementary lighting) as a treatment to break dormancy (Nienstaedt 1966,1967). At the end of the second growing season these final measurements were taken:

1. final height
2. diameter (at first internode)
3. number of branches

The seedlings were then destructively sampled to determine:

4. total fresh weight
5. total dry weight
6. top fresh weight
7. top dry weight
8. fresh weight root-to-shoot ratio
9. dry weight root-to-shoot ratio
10. top dry weight to top fresh weight ratio (relative dry matter)
11. total dry weight to total fresh weight ratio (relative dry matter)

The factorial design of this experiment facilitated the use of analysis of variance (ANOVA). Effects were partitioned into two treatments (i.e. environments), 27 sources (i.e. populations) and the interaction of sources and treatments. The analyses of the data were carried out in two sections:

1. First season results:
   a. ANOVA of final first season heights,
   b. correlation analyses of final first season heights, on environmental parameters (latitude, longitude, elevation and converted latitudes (Wiersma 1964)),
   c. ANOVA of first season height growth

2. Final results:
   a. ANOVA of second season height growth and all final measurements,
   b. correlation analysis of measurements showing statistical significance ($P \leq .05$) among sources within treatments using environmental parameters as independent variables,
   c. Duncan's Multiple Range Test of measurements showing ANOVA statistical significance ($P \leq .05$) among sources within treatments,
   d. principal components analysis using all final measurements.

III. Results and Analyses

First Season Results

Analysis of variance of seedling heights at the end of the first growing season indicated a significant ($P \leq 0.001$) difference existed between treatments. However, no significant differences could be detected among sources within treatments (Table 2).

There were no significant correlations of first season final heights on latitude, longitude, elevation and converted latitudes in either growth regime (Table 3).

Analysis of growth at bi-weekly intervals (expressed as a percentage of first season final height) using analysis of variance indicated that significant ($P \leq 0.001$) differences existed among growth periods in both environments. However, no significant differences were evident among sources within either environment (Tables 4 and 5).

Second Season Results

Analysis of variance of all final measurements indicated that there were significant ($P \leq 0.05$) differences among sources with respect to three measures. Total relative dry matter or the ratio of total dry weight to total fresh weight, top relative dry matter or the ratio of top dry weight to top fresh weight, and number of branches per

SOURCE OF VARIATION	Df	S.S.	M.S.	F	PROBABILITY
ENVIRONMENT (E)	1	151.167	151.167	81.005	0.001
SOURCE (S)	26	38.731	1.490	0.798	0.741
ExS	26	42.117	1.620	0.868	0.650
ERROR	108	201.544	1.866		

Table 2. Analysis of variance of first season final heights using replicate means for 27 white spruce sources (six seedlings per replicate, three replicates per environment, and two environments) (no missing cases).

NORTHERN ENVIRONMENT	SOUTHERN ENVIRONMENT
1. HEIGHT VS. LATITUDE: r= -0.13 N.S.	1. HEIGHT VS. LATITUDE: r= -0.03 N.S.
2. HEIGHT VS. LONGITUDE: r= -0.23 N.S.	2. HEIGHT VS. LONGITUDE: r= -0.13 N.S.
3. HEIGHT VS. ELEVATION: r= 0.10 N.S.	3. HEIGHT VS. ELEVATION: r= -0.09 N.S.
4. HEIGHT VS. CONVERTED LATITUDE: r= 0.02 N.S.	4. HEIGHT VS. CONVERTED LATTITUDE: r= -0.21 N.S.

TABLE 3. Significance of correlations of first season final heights on latitude, longitude elevation and converted latitude of 27 white spruce sources. N.S. - not significant, *-$P \leq 0.10$, **$P \leq 0.05$, ***-$P \leq 0.01$.

SOURCE OF VARIATION	Df	S.S.	M.S.	F	PROBABILITY
SOURCES	26	27673.398	1064.382	1.498	0.088
ERROR	79	56133.000	710.544		
HEIGHT PERIODS	6	313126.875	52187.813	917.75	0.001
SOURCES x HEIGHT PERIODS	156	11020.387	70.643	1.242	0.043
ERROR	474	26954.000	56.865		

Table 4. Analysis of variance of first season height growth in the southern environment using replicate means for 27 white spruce sources (four replicates, seven height growth periods) (two missing cases).

SOURCE OF VARIATION	Df	S.S.	M.S.	F	PROBABILITY
SOURCES	26	11183.895	430.15	0.842	0.678
ERROR	53	27079.000	510.924		
HEIGHT PERIODS	3	80287.563	26762.52	233.432	0.001
SOURCES x HEIGHT PERIODS	78	7898.238	101.259	0.883	0.728
ERROR	159	18229.000	114.648		

Table 5. Analysis of variance of first season height growth in northern environment using replicate means for 27 white spruce sources (three replicates, four height growth periods) (one missing case).

individual showed significant differences among sources within treatments (Tables 6, 7, 8, 9 and 10).

Correlations analysis of all characters with respect to all environmental parameters indicated that only total and top relative dry matter and number of branches had significant correlations (Tables 11,12,13,14 and 15). The trends with respect to total relative dry matter and top relative dry matter differed only slightly between environments. Total relative dry matter in both environments decreased with increasing converted latitudes; decreased with increasing elevation; and, in the southern environment only, increased with increasing latitude of the source. There was no significant ($P \leq 0.05$) relationship between top relative dry matter and converted latitude; but significant relationships, similar to that of total relative dry matter were evident with respect to elevation and latitude of the source (Figures 4 through 12). Number of branches decreased with increasing converted latitudes; however, this relationship was only significant ($P \leq 0.001$) in the southern environment (Figure 13,14).

Analysis of total and top relative dry matter as well as number of branches using Duncan's Multiple Range Test showed some significant ($P \leq 0.05$) groupings of sources in both environments (Figures 15, 16 and 17). These groupings are more clearly illustrated on source map plots (Figures 18 to 23).

TOP RELATIVE
DRY MATTER (g./g.)

	NORTHERN ENVIRONMENT		SOUTHERN ENVIRONMENT	
SOURCES	MEAN	STD. DEV.	MEAN	STD. DEV.
1	0.394	0.062	0.353	0.047
2	0.366	0.013	0.344	0.042
3	0.361	0.022	0.362	0.026
4	0.372	0.013	0.374	0.025
5	0.345	0.017	0.354	0.013
6	0.364	0.002	0.382	0.016
7	0.345	0.005	0.402	0.013
8	0.399	0.016	0.382	0.029
10M	0.373	0.024	0.364	0.029
10H	0.350	0.020	0.333	0.036
10L	0.377	0.013	0.360	0.022
13L	0.343	0.016	0.354	0.016
13M	0.362	0.029	0.359	0.033
13H	0.321	0.014	0.336	0.030
16L	0.357	0.018	0.371	0.010
16M	0.329	0.005	0.326	0.036
16H	0.362	0.016	0.341	0.031
18	0.358	0.008	0.362	0.016
19	0.345	0.020	0.387	0.008
20	0.348	0.008	0.366	0.025
21	0.362	0.005	0.411	0.011
22	0.376	0.025	0.380	0.042
23	0.341	0.002	0.428	0.051
24	0.366	0.014	0.395	0.002
25	0.411	0.045	0.381	0.018
26	0.382	0.019	0.377	0.005
27	0.386	0.035	0.384	0.022

Table 6. Means and standard deviations of total and top relative dry matter and number of branches for 27 sources of white spruce grown in two environments.

	NUMBER OF BRANCHES			
	NORTHERN ENVIRONMENT		SOUTHERN ENVIRONMENT	
SOURCES	MEAN	STD. DEV.	MEAN	STD. DEV.
1	10.722	2.299	10.667	2.186
2	9.333	4.126	14.500	4.822
3	10.322	1.329	13.222	1.836
4	7.167	2.323	10.922	2.149
5	8.633	2.205	11.356	2.044
6	6.483	2.202	10.989	1.673
7	7.789	3.383	11.300	3.291
8	6.222	0.977	8.244	0.518
10M	8.000	2.843	9.083	0.589
10H	6.917	1.673	6.117	3.233
10L	7.256	1.611	9.717	0.861
13L	6.167	1.167	5.944	1.549
13M	6.183	1.643	10.889	0.192
13H	7.500	1.803	5.156	2.734
16L	12.500	1.803	14.389	1.512
16M	7.467	1.910	9.667	1.155
16H	8.000	1.000	9.417	2.097
18	7.222	0.839	9.000	1.803
19	8.761	2.115	12.200	0.800
20	11.111	2.457	8.950	2.642
21	7.178	0.500	8.467	0.503
22	6.989	2.474	10.211	3.322
23	5.917	1.296	9.472	1.528
24	8.111	1.262	8.000	0.126
25	9.450	1.485	9.889	1.836
26	9.556	2.084	8.333	1.756
27	9.317	0.988	6.667	0.882

Table 6. (continued)

TOTAL RELATIVE
DRY MATTER (g./g.)

	NORTHERN ENVIRONMENT		SOUTHERN ENVIRONMENT	
SOURCES	MEAN	STD. DEV.	MEAN	STD. DEV.
1	0.387	0.083	0.274	0.062
2	0.355	0.025	0.272	0.011
3	0.314	0.017	0.247	0.005
4	0.333	0.024	0.271	0.037
5	0.308	0.011	0.267	0.005
6	0.306	0.005	0.297	0.031
7	0.304	0.008	0.311	0.023
8	0.343	0.013	0.291	0.018
10M	0.328	0.004	0.284	0.019
10H	0.267	0.036	0.245	0.026
10L	0.327	0.028	0.270	0.016
13L	0.312	0.008	0.276	0.004
13M	0.324	0.030	0.267	0.011
13H	0.269	0.024	0.258	0.022
16L	0.310	0.039	0.298	0.007
16M	0.289	0.008	0.266	0.025
16H	0.291	0.031	0.233	0.043
18	0.303	0.015	0.292	0.017
19	0.314	0.012	0.301	0.021
20	0.298	0.011	0.262	0.020
21	0.319	0.015	0.310	0.002
22	0.320	0.019	0.295	0.028
23	0.283	0.008	0.269	0.020
24	0.315	0.008	0.302	0.003
25	0.325	0.002	0.286	0.011
26	0.289	0.015	0.262	0.016
27	0.290	0.040	0.304	0.013

Table 6. (continued)

	Total Relative Dry Matter	Top Relative Dry Matter	Number of Branches
Environment (E)	0.001	0.112	0.001
Source (S)	0.001	0.001	0.001
ExS	0.016	0.018	0.043

Table 7. Summary table of analysis of variance probability values for total and top relative dry matter and number of branches for 27 sources of white spruce grown in two environments.

SOURCE OF VARIATION	Df	S.S.	M.S.	F	PROBABILITY
ENVIRONMENT (E)	1	.044	.044	70.952	0.001
SOURCE (S)	26	.050	.002	3.055	0.001
ExS	26	.030	.001	1.848	0.016
ERROR	103	.064	.001		

Table 8. Analysis of variance of total relative dry matter using replicate means (three replicates per environment and two environments) for 27 white spruce sources (five missing cases).

SOURCE OF VARIATION	Df	S.S.	M.S.	F	PROBABILITY
ENVIRONMENT (E)	1	.002	.002	2.568	0.112
SOURCE (S)	26	.046	.002	2.850	0.001
ExS	26	.029	.001	1.826	0.018
ERROR	103	.064	.001		

Table 9. Analysis of variance of top relative dry matter using replicate means (three replicates per environment and two environments) for 27 white spruce sources (five missing cases).

SOURCE OF VARIATION	Df	S.S.	M.S.	F	PROBABILITY
ENVIRONMENT (E)	1	96.741	96.741	26.679	0.001
SOURCE (S)	26	438.608	16.870	3.955	0.001
ExS	26	181.527	6.982	1.637	0.043
ERROR	104	443.641	4.266		

Table 10. Analysis of variance of number of branches using replicate means (three replicates per environment and two environments) for 27 white spruce sources (four missing cases).

	Latitude	Elevation	Converted Latitude
Total Relative Dry Matter	0.09	-0.41**	-0.67***
Top Relative Dry Matter	0.35*	-0.47**	-0.34*
Number of Branches	-0.04	-0.10	-0.19

Table 11. Summary table of correlations of total and top relative dry matter and number of branches versus latitude, elevation and converted latitude of the source (27 sources of white spruce grown in a simulated northern Alberta environment).

	Latitude	Elevation	Converted Latitude
Total Relative Dry Matter	0.54***	-0.65***	-0.49***
Top Relative Dry Matter	0.64***	-0.62***	-0.25
Number of Branches	0.04	0.12	-0.50***

Table 12. Summary table of correlations of total and top relative dry matter and number of branches versus latitude, elevation and converted latitude of the source (27 sources of white spruce grown in a simulated southern Alberta environment).

NORTHERN ENVIRONMENT	SOUTHERN ENVIRONMENT
1. TOTAL RELATIVE DRY MATTER VS. ELEVATION: r= -0.409**	1. TOTAL RELATIVE DRY MATTER VS. ELEVATION: r= -0.645***
2. TOTAL RELATIVE DRY MATTER VS. CONVERTED LATITUDE: r= -0.671***	2. TOTAL RELATIVE DRY MATTER VS. CONVERTED LATITUDE: r= -0.489***
3. TOTAL RELATIVE DRY MATTER VS. LATITUDE: r= 0.089 N.S.	3. TOTAL RELATIVE DRY MATTER VS.LATITUDE: r= 0.537***

Table 13. Significance of correlations of total relative dry matter on latitude, elevation and converted latitude of 27 white spruce sources.

NORTHERN ENVIRONMENT	SOUTHERN ENVIRONMENT
1. TOP RELATIVE DRY MATTER VS. ELEVATION: r= -0.466**	1. TOP RELATIVE DRY MATTER VS. ELEVATION: r= -0.618***
2. TOP RELATIVE DRY MATTER VS. CONVERTED LATITUDE: r= -0.335*	2. TOP RELATIVE DRY MATTER VS. CONVERTED LATITUDE: r= -0.248 N.S.
3. TOTAL RELATIVE DRY MATTER VS. LATITUDE: r= 0.347*	3. TOTAL RELATIVE DRY MATTER VS. LATITUDE: r= 0.644***

Table 14. Significance of correlations of top relative dry matter on latitude, elevation and converted latitude of 27 white spruce sources.

NORTHERN ENVIRONMENT	SOUTHERN ENVIRONMENT
1. NUMBER OF BRANCHES VS. ELEVATION: r= -0.097 N.S.	1. NUMBER OF BRANCHES VS. ELEVATION: r= -0.124 N.S.
2. NUMBER OF BRANCHES VS. CONVERTED LATITUDE: r= -0.194 N.S.	2. NUMBER OF BRANCHES VS. CONVERTED LATITUDE: r= -0.503***
3. NUMBER OF BRANCHES VS. LATITUDE: r= 0.035 N.S.	3. NUMBER OF BRANCHES VS. LATITUDE: r= 0.036 N.S.

Table 15. Significance of correlations of number of branches on latitude, elevation and converted latitude of 27 white spruce sources.

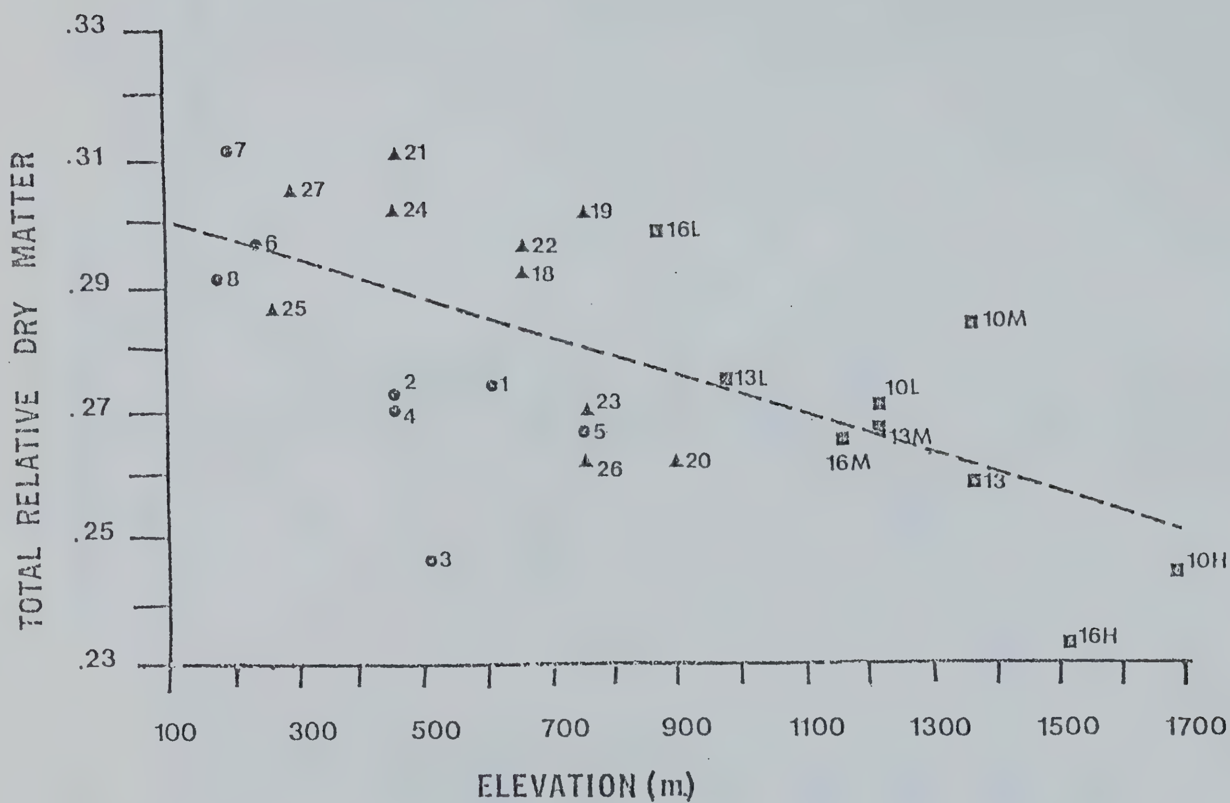

Figure 4. Relationship of total relative dry matter (dry weight (g)/fresh weight (g)) and elevation of 27 white spruce sources grown in a simulated southern Alberta environment (r = -0.645, Y = 0.302 - 0.00003x).

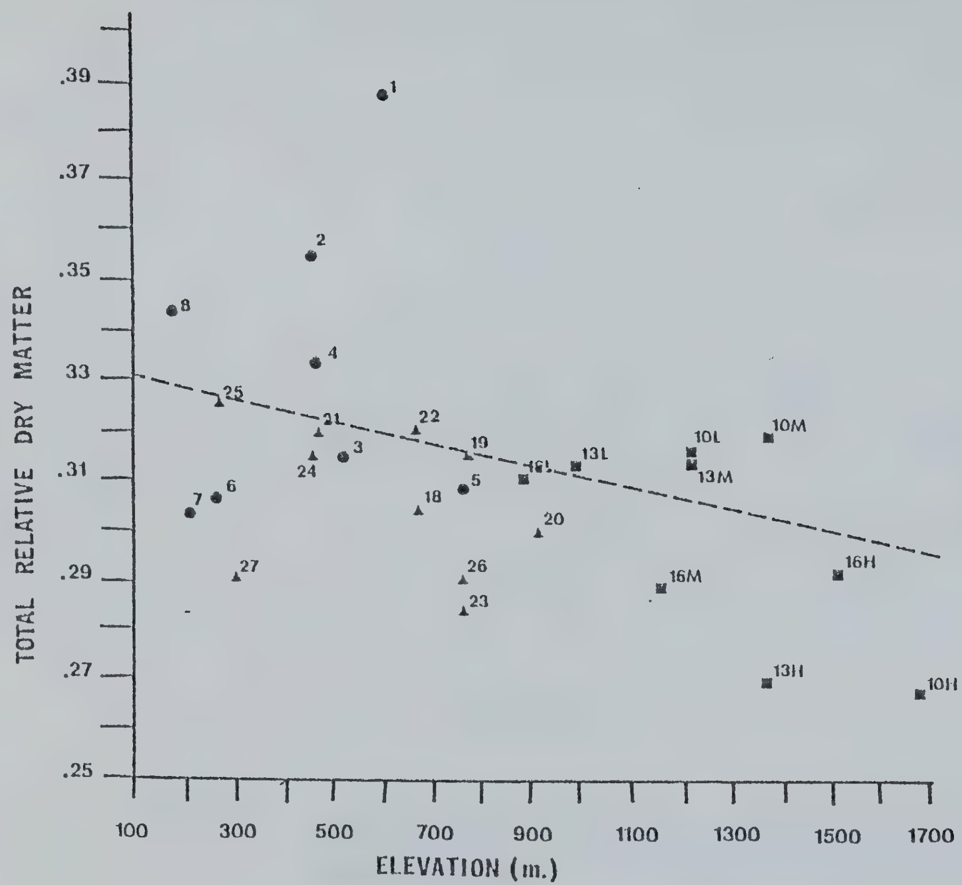

Figure 5. Relationship of total relative dry matter and elevation of 27 white spruce sources grown in a simulated northern Alberta environment. ($r = -0.409$, $Y = 0.331 - 0.00002x$).

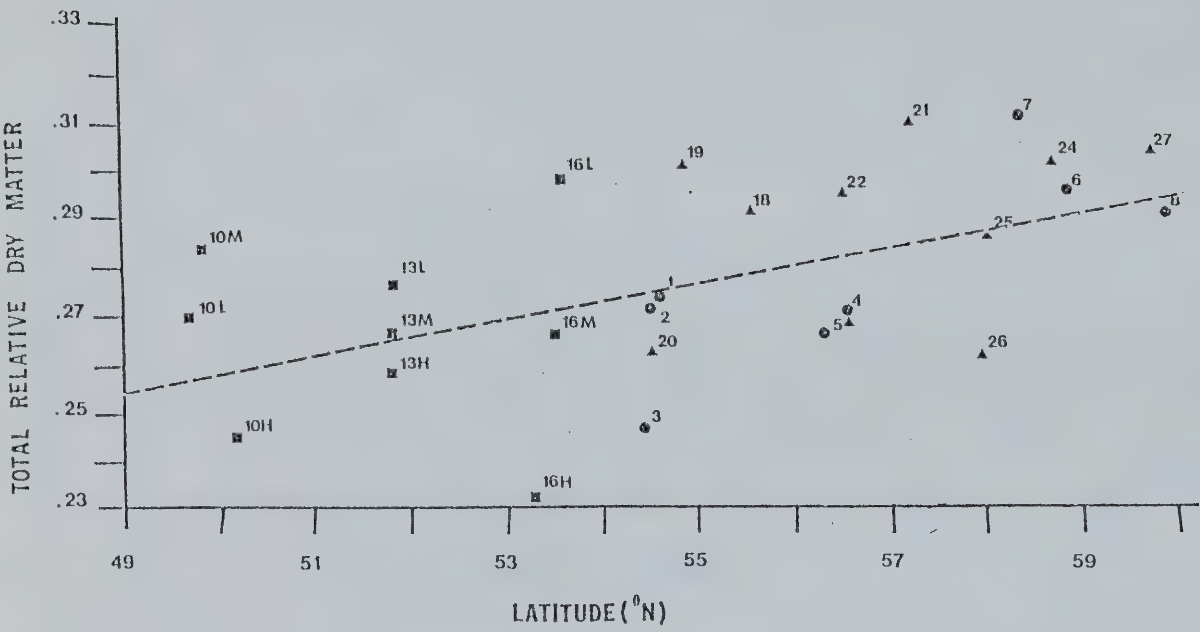

Figure 6. Relationship of total relative dry matter and latitude of 27 white spruce sources grown in a simulated southern Alberta environment (r = 0.537, Y = 0.074 + 0.0037x).

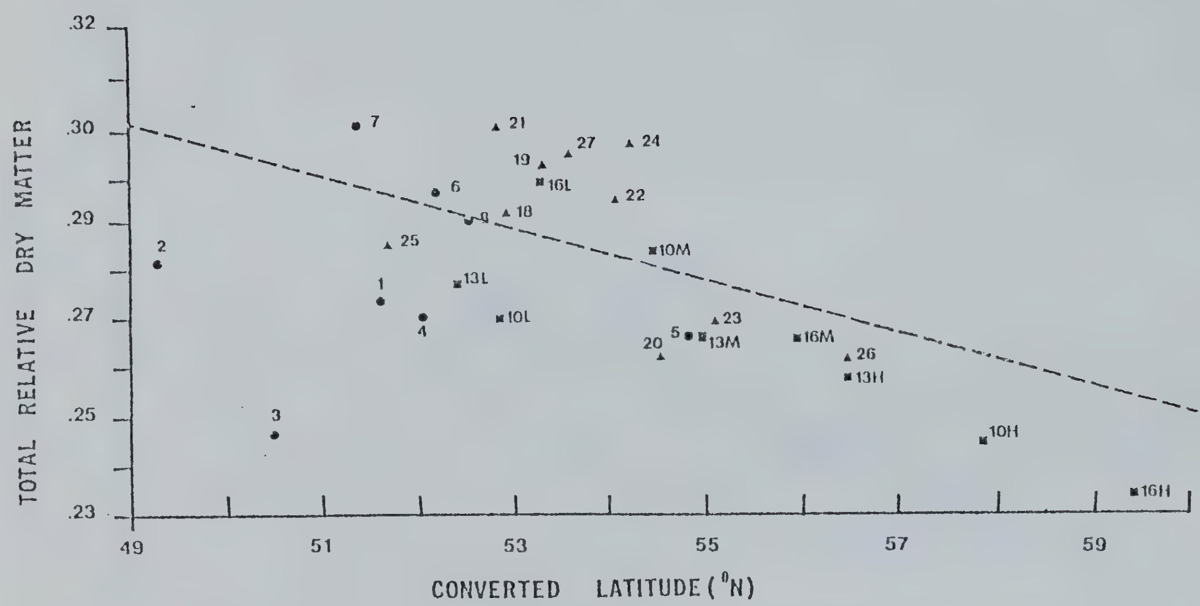

Figure 7. Relationship of total relative dry matter and converted latitude of 27 white spruce sources grown in a simulated southern Alberta environment (r = -0.489, Y = 0.535 - 0.045x).

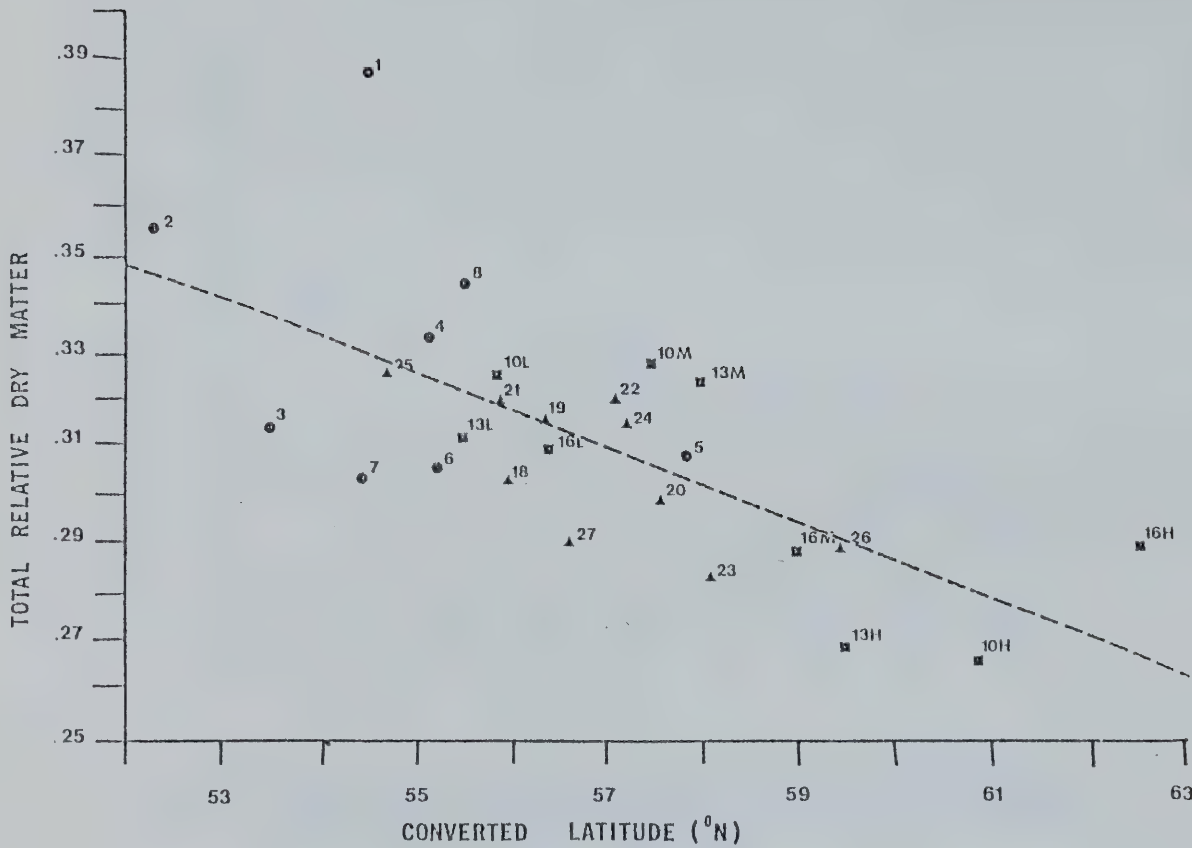

Figure 8. Relationship of total relative dry matter and converted latitude of 27 white spruce sources grown in a simulated northern Alberta environment ($r = -0.671$, $Y = 0.748 - 0.0077x$).

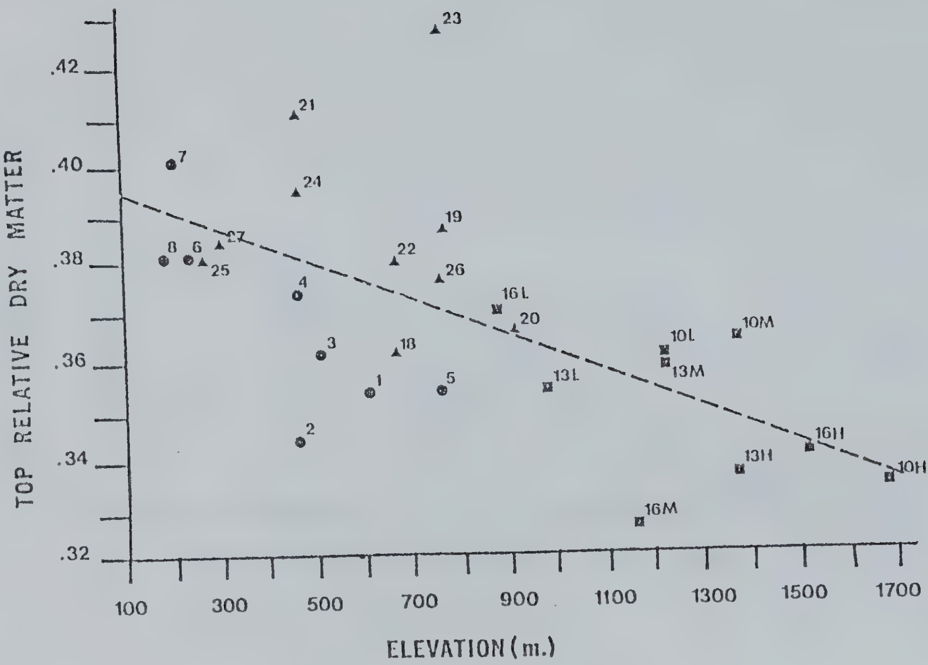

Figure 9. Relationship of top relative dry matter (dry weight (g)/ fresh weight (g)) and elevation of 27 white spruce sources grown in a simulated southern Alberta environment ($r = -0.618$, $Y = 0.396 - 0.000035x$).

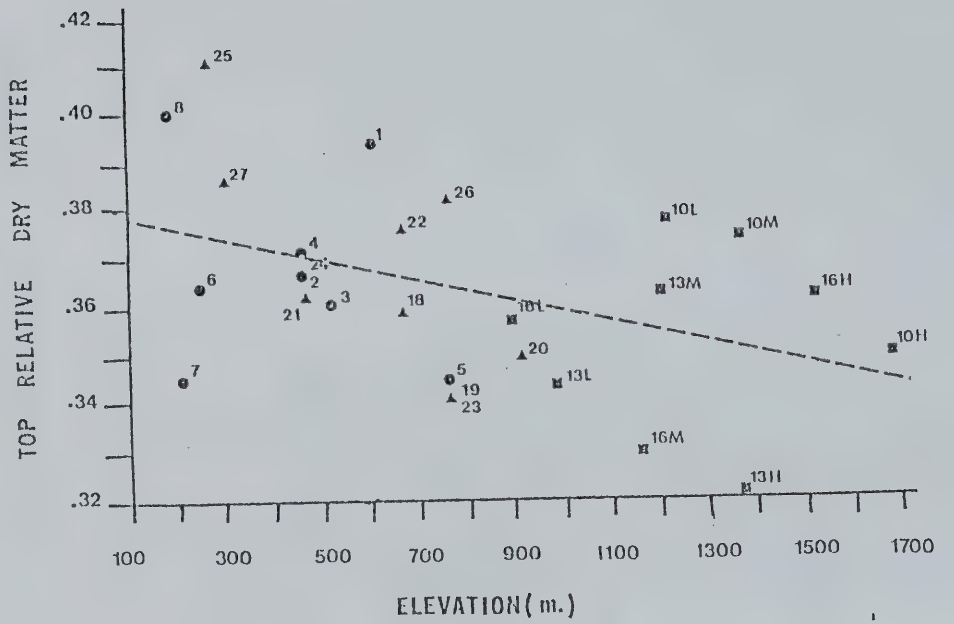

Figure 10. Relationship of top relative dry matter and elevation of 27 white spruce sources grown in a simulated northern Alberta environment ($r = -0.496$, $Y = 0.38 - 0.00002x$).

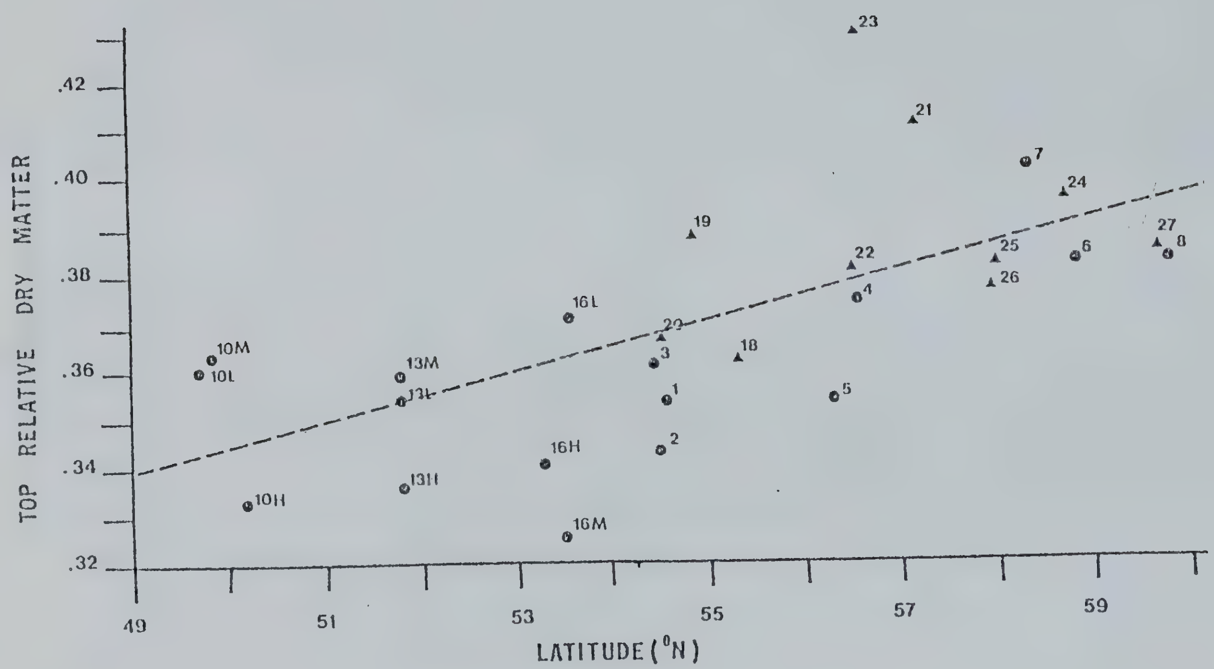

Figure 11. Relationship of top relative dry matter and latitude of 27 white spruce sources grown in a simulated southern Alberta environment (r = 0.644, Y = 0.085 + 0.0052x).

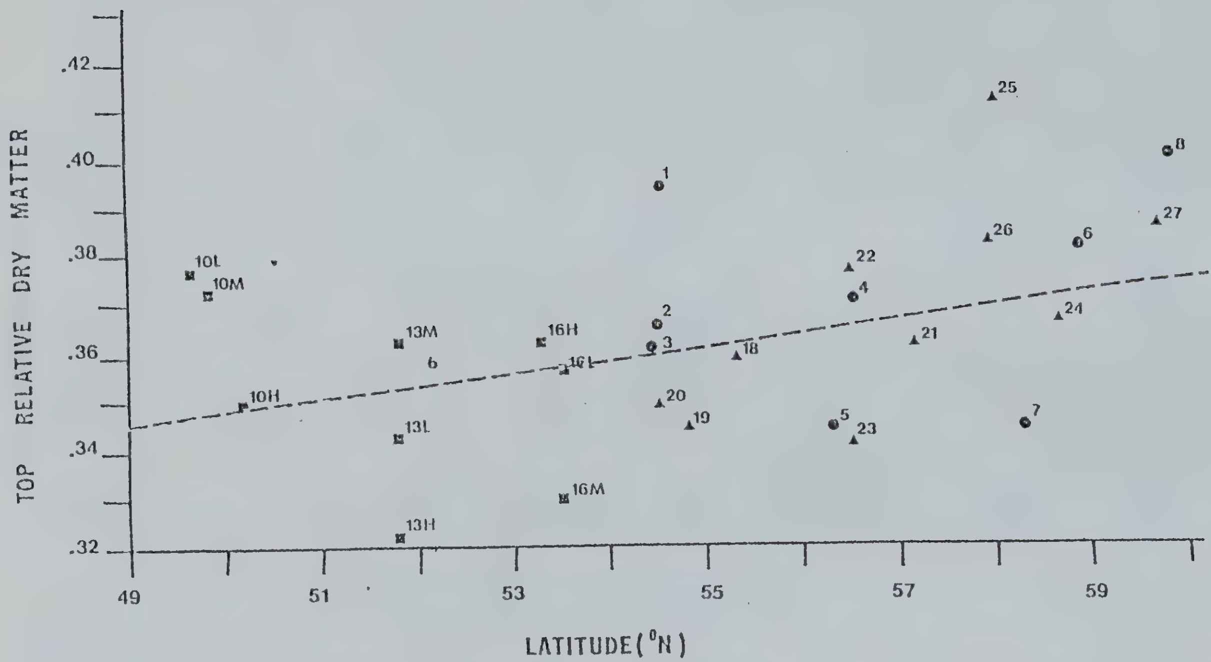

Figure 12. Relationship of top relative dry matter and latitude of 27 white spruce sources grown in a simulated northern Alberta environment ($r = 0.374$, $Y = 0.219 + 0.0026x$).

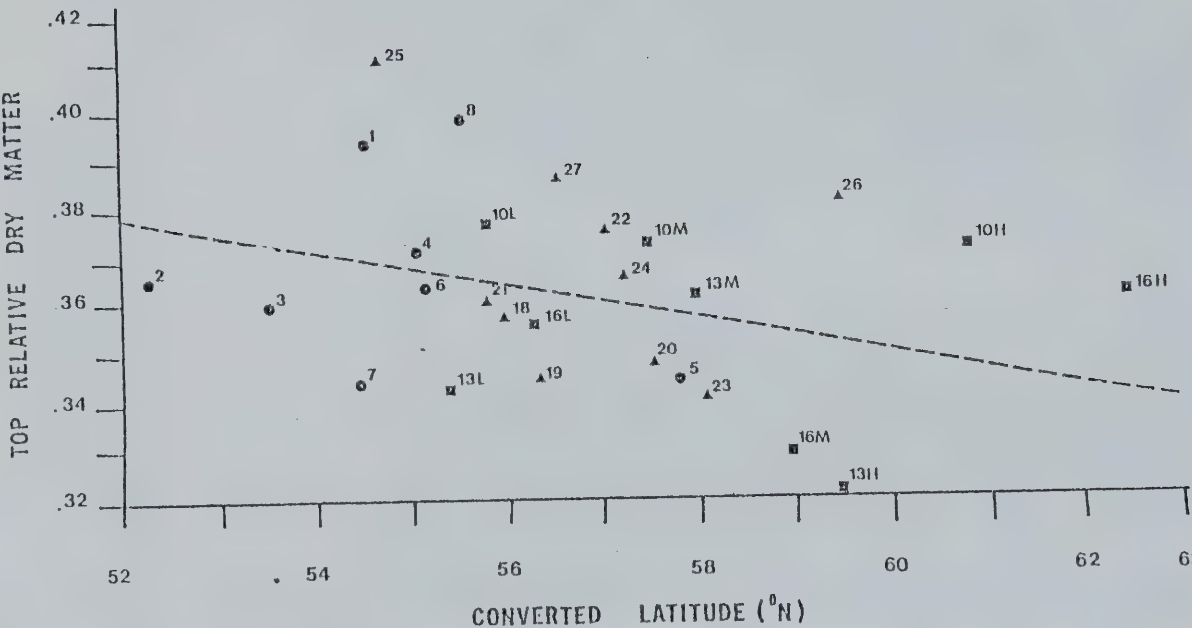

Figure 13. Relationship of top relative dry matter and converted latitude of 27 white spruce sources grown in a simulated northern Alberta environment (r = -0.335, Y = 0.54 - 0.0031x).

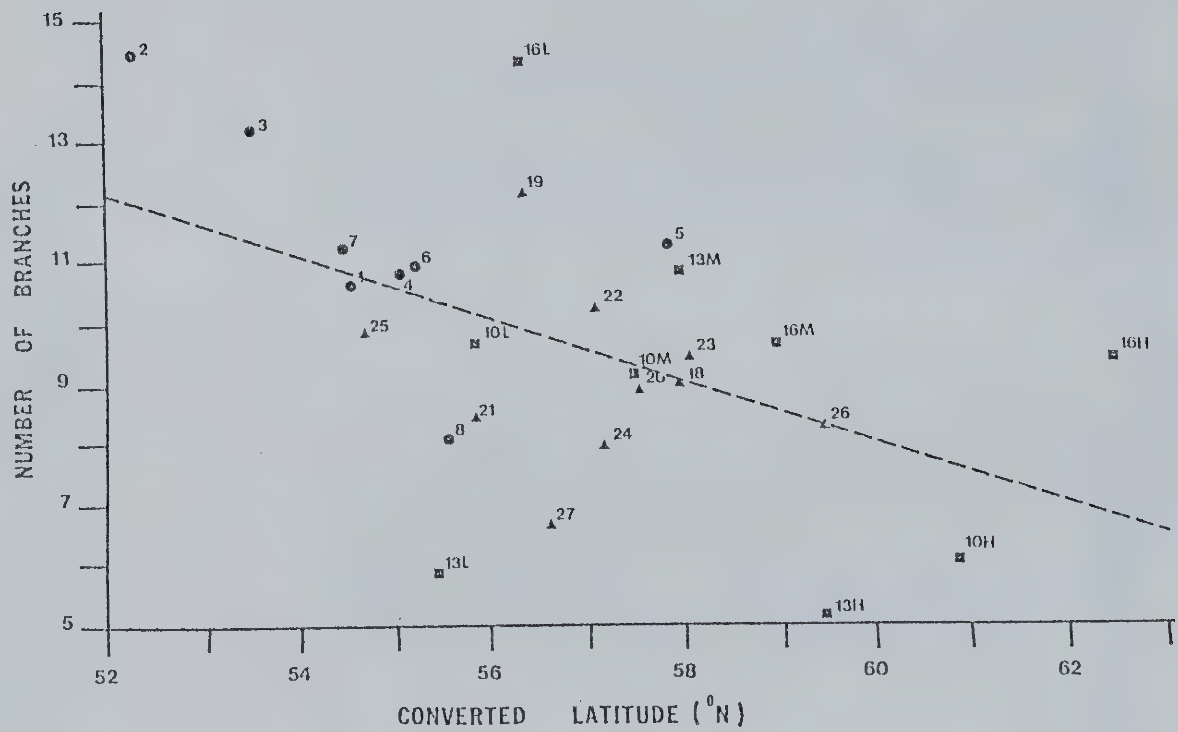

Figure 14. Relationship of number of branches and converted latitude of 27 white spruce sources grown in a simulated southern Alberta environment ($r = -0.503$, $Y = 39.68 - 0.528x$).

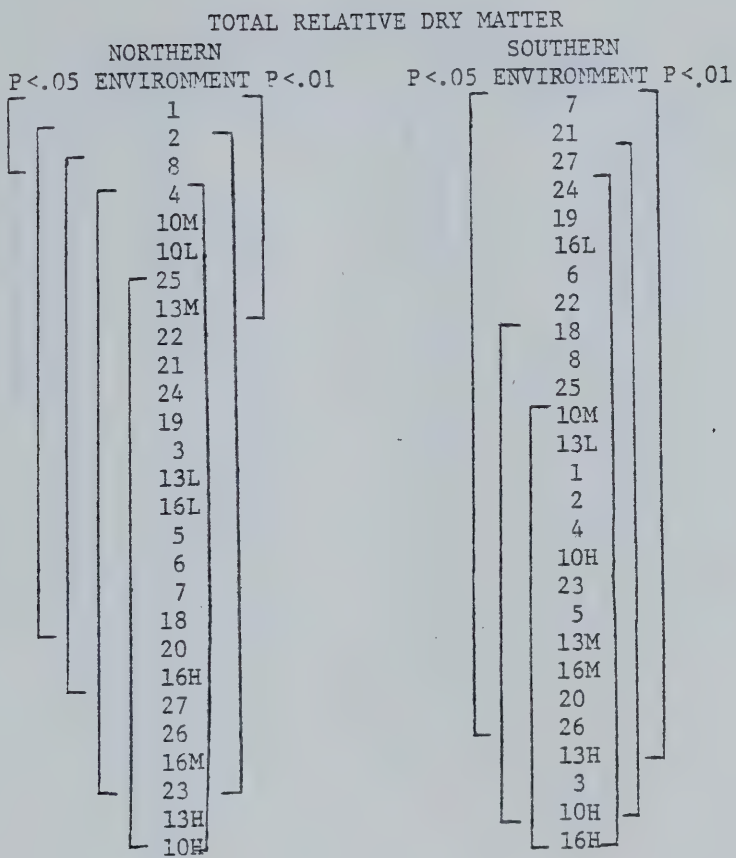

Figure 15. Results of Duncan's Multiple Range Test on total relative dry matter for 27 white spruce sources grown in two test environments. Sources not included within the same line were significantly different at the five or one percent level.

TOP RELATIVE DRY MATTER

NORTHERN	SOUTHERN
P<.05 ENVIRONMENT P<.01	P<.05 ENVIRONMENT P<.01
25	23
8	21
1	7
27	24
26	19
10L	27
22	8
10M	6
4	25
24	22
2	26
6	4
13M	16L
21	20
16H	10M
3	3
18	18
16L	10L
10H	13M
20	5
7	13L
5	1
19	2
13L	16H
23	13H
16M	10H
13H	16M

Figure 16. Results of Duncan's Multiple Range Test on top relative dry matter for 27 white spruce sources grown in two test environments. Sources not included within the same line were significantly different at the five or one percent level.

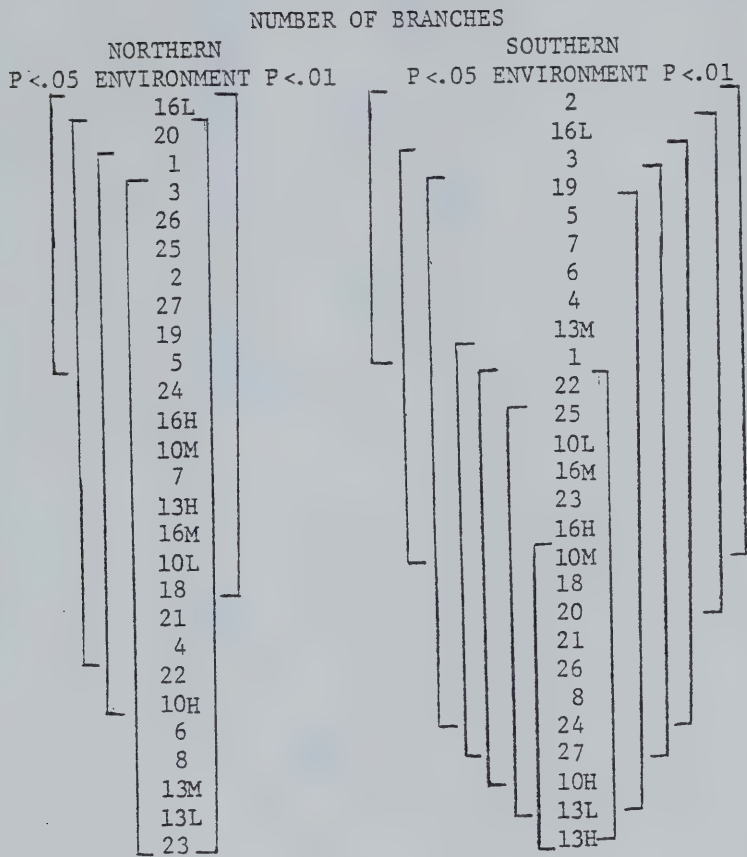

Figure 17. Results of Duncan's Multiple Range Test on number of branches for 27 white spruce sources grown in two test environments. Sources not included within the same line were significantly different at the five or one percent level.

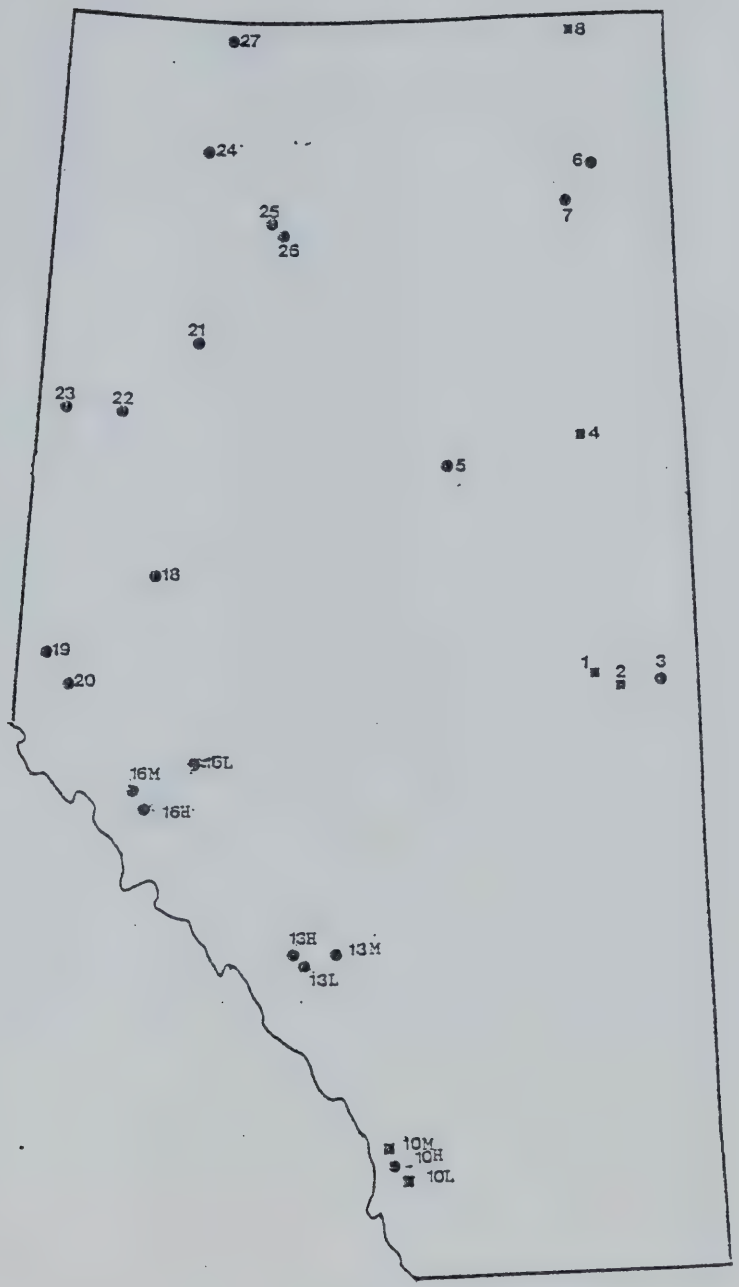

Figure 18. Source map of Duncan's Multiple Range Test results for total relative dry matter of 27 white spruce sources grown in the northern environment. (■ source means are significantly different from ●)

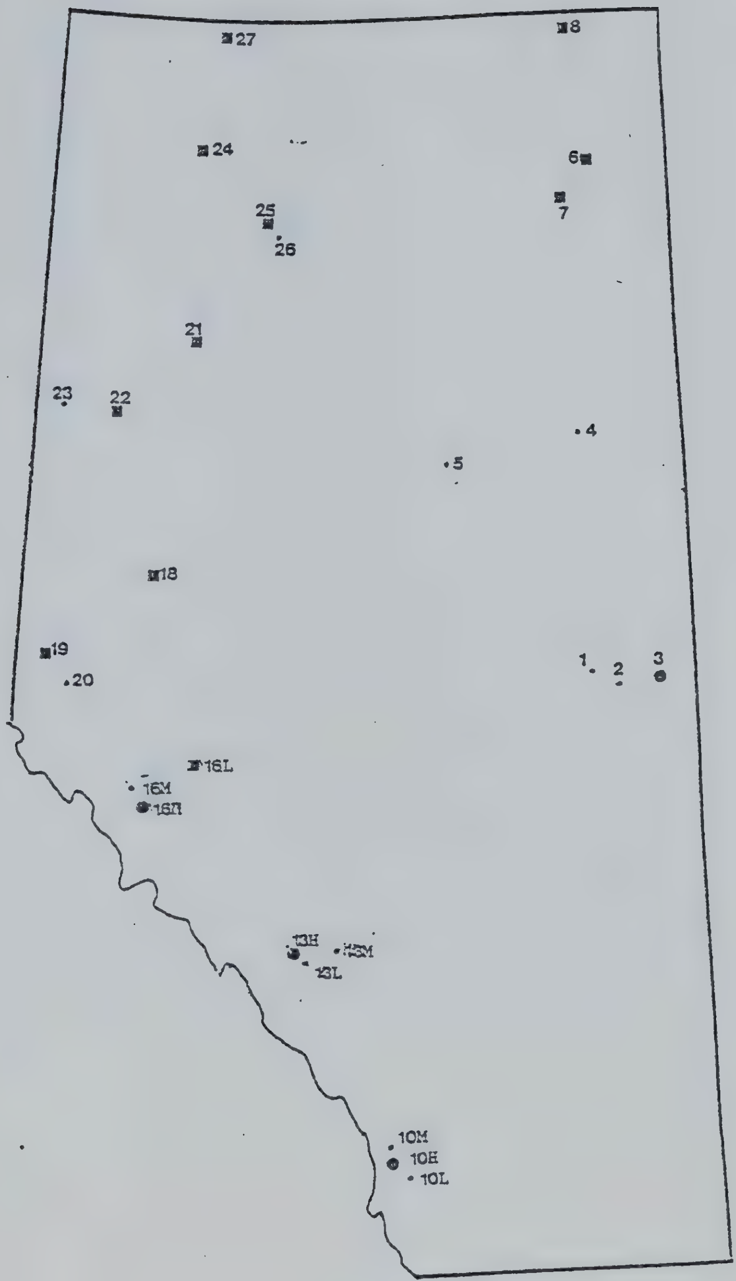

Figure 19. Source map of Duncan's Multiple Range Test results for total relative dry matter of 27 white spruce sources grown in the southern environment. (■ source means are significantly different from ●)

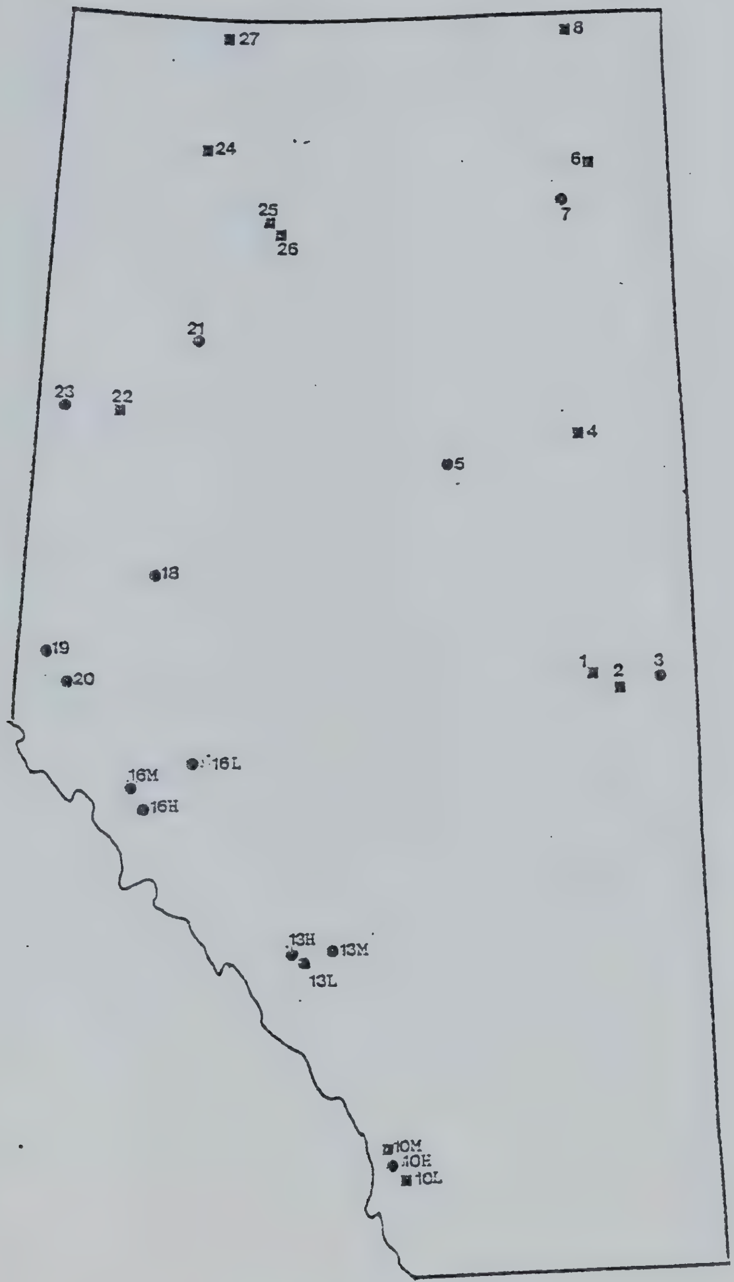

Figure 20. Source map of Duncan's Multiple Range Test results for top relative dry matter of 27 white spruce sources grown in the northern environment. (■ source means are significantly different from ●)

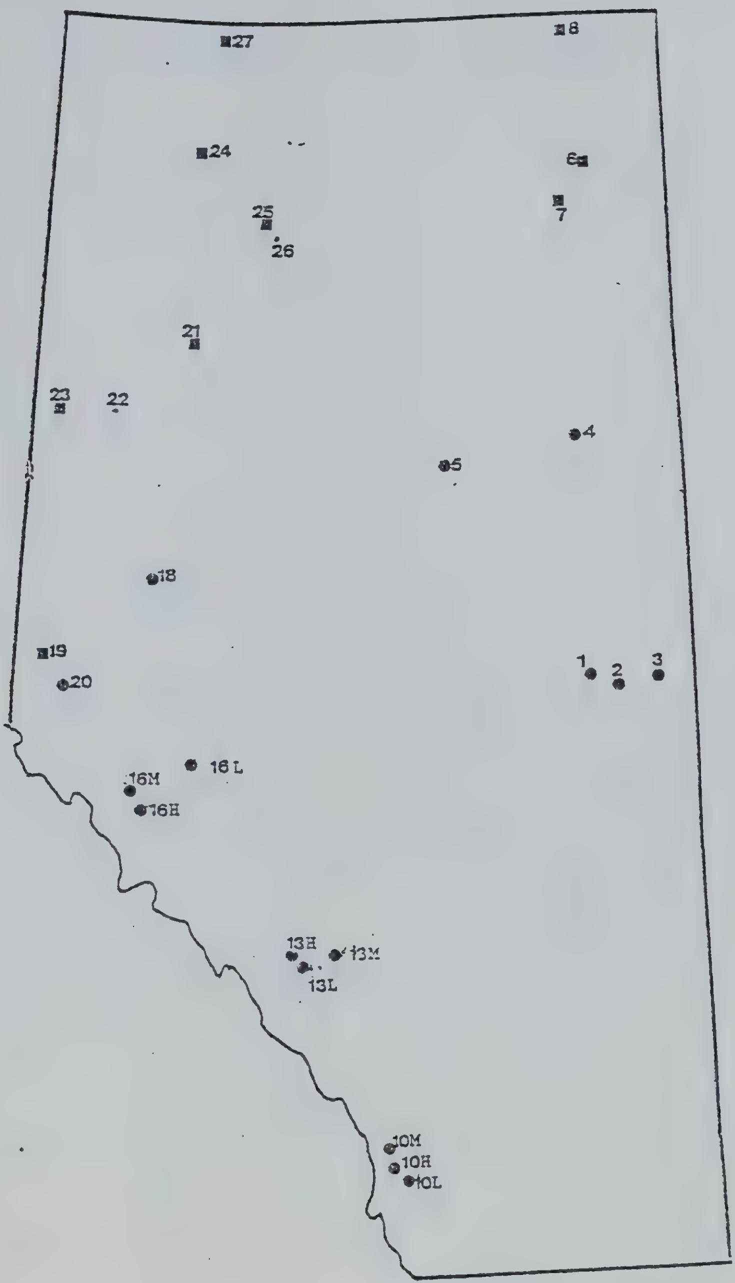

Figure 21. Source map of Duncan's Multiple Range Test results for top relative dry matter of 27 white spruce sources grown in the southern environment. (■ source means are significantely different from ●)

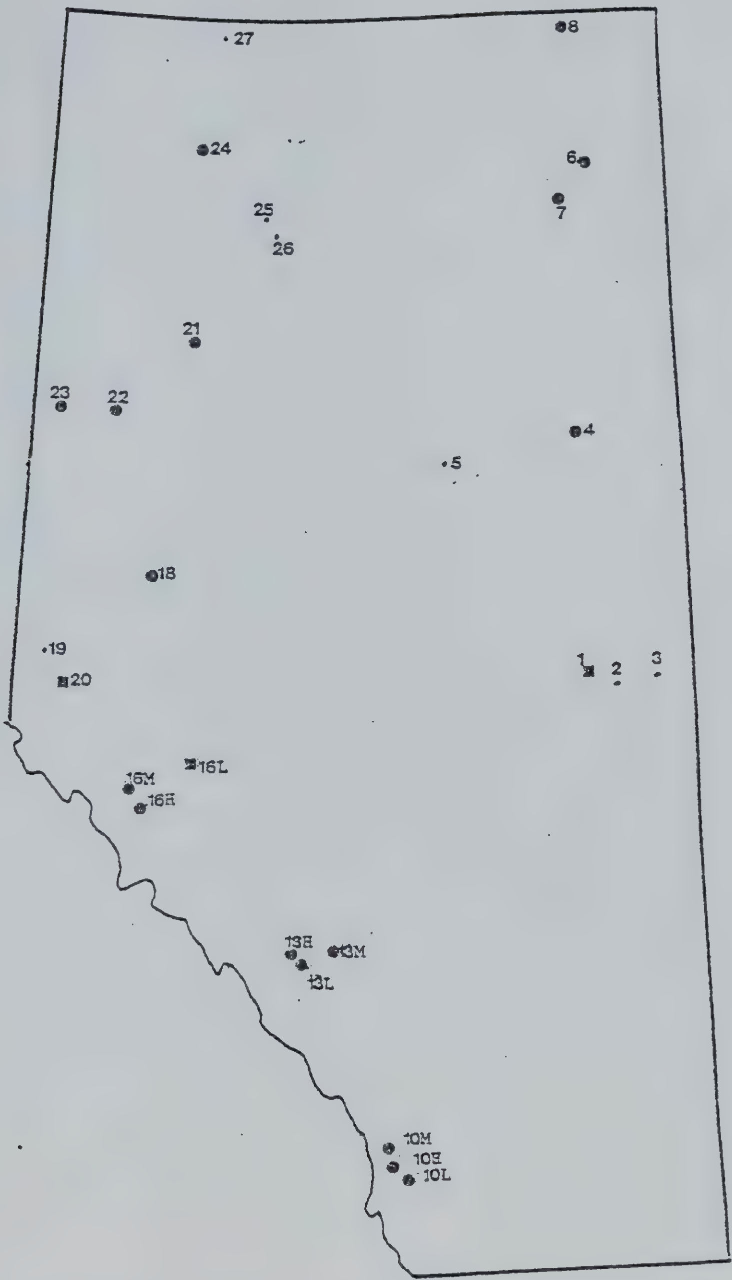

Figure 22. Source map of Duncan's Multiple Range Test results for number of branches of 27 white spruce sources grown in the northern environment.
(■ source means are significantly different from ●)

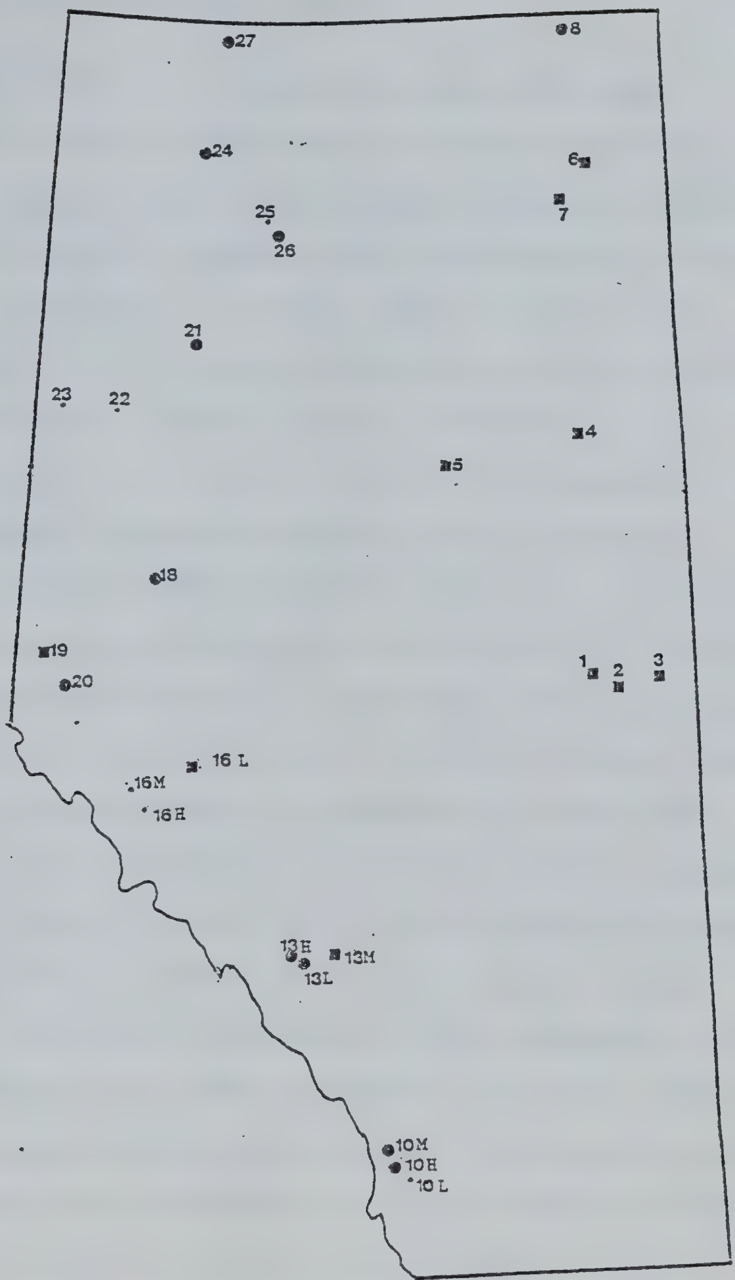

Figure 23. Source map of Duncan's Multiple Range Test results for number of branches of 27 white spruce sources grown in the southern environment.
(■ source means are significantly different from ●)

Sources not designated as significantly different are not significantly different from each other, and from at least one of the two significant groups.

Source means of all characteristics from both environments were analyzed using principal components analysis (PCA). PCA is a multivariate statistical technique which can be used to summarize many independent variables into fewer artificial variables. "Each component is a weighted sum of the original variables. The first principal component accounts for the largest percentage of the variance present in a set of multivariate observations. The second principal component accounts for the largest percentage of the remaining variation", and so on until all the variation has been accounted for (Dancik and Barnes 1975). Analysis of all final measurements indicated that three principal components could be used to account for a significant (eigenvalues ≥1.0; Isebrand and Crow 1975) proportion of the variation among sources within either environment (Tables 16 and 17). In the northern environment the first principal component was essentially a size component, the second a root/shoot ratio component, and the third a relative dry matter component (Table 18). These three components accounted for 84.5% of the variation among sources within this environment. In the southern environment the first principal component was essentially a size component, the second a root/shoot ratio component, and the third a relative dry matter component (Table 19). These

Principal Component	Eigenvalue	Percentage of Variation	Cumulative Percentage
1	5.411	49.2	49.2
2	2.499	22.7	71.9
3	1.387	12.6	84.5

Table 16. Eigenvalues of, and percentage of variation accounted for by, principal component axes derived from 11 characters of 27 sources of white spruce (northern environment).

Principal Component	Eigenvalue	Percentage of Variation	Cumulative Percentage
1	5.813	52.8	52.8
2	1.993	18.1	71.0
3	1.703	15.5	86.4

Table 17. Eigenvalues of, and percentage of variation accounted for by, principal component axes derived from 11 characters of 27 sources of white spruce (southern environment).

Character	Principal Component 1	Principal Component 2	Principal Component 3
Final height	0.148	-0.146	0.061
Diameter	0.153	0.065	-0.015
Number of branches	0.139	-0.191	-0.025
Total fresh weight	0.167	0.118	-0.110
Top fresh weight	0.204	-0.064	-0.130
Total dry weight	0.182	-0.015	0.040
Top dry weight	0.165	0.075	0.067
Fresh weight R/S	-0.043	0.415	0.037
Dry weight R/S	-0.014	0.412	0.119
Total relative dry matter	-0.006	-0.090	0.461
Top relative dry matter	-0.070	0.184	0.606

Table 18. Coefficients of all characters used in calculating the first three principal components of 27 white spruce sources grown in the northern environment.

Character	Principal Component 1	Principal Component 2	Principal Component 3
Final height	0.148	-0.199	0.064
Diameter	0.146	0.138	-0.067
Number of branches	0.142	-0.123	-0.028
Total fresh weight	0.173	0.099	-0.117
Top fresh weight	0.184	-0.055	-0.065
Total dry weight	0.165	-0.014	0.065
Top dry weight	0.157	0.059	0.064
Fresh weight R/S	-0.005	0.456	-0.071
Dry weight R/S	-0.044	0.410	0.103
Total relative dry matter	-0.045	-0.101	0.544
Top relative dry matter	-0.032	0.154	0.479

Table 19. Coefficients of all characters used in calculating the first three principal components of 27 white spruce sources grown in the northern environment.

three principal components accounted for 86.4% of the variation among sources in the southern environment.

Ordination of sources in three-dimensional multivariate space using principal component scores did not indicate any significant groupings.

The 27 white spruce sources tested have coefficients of variation for total and top relative dry matter ranging from 5.8% to 8.0% (Table 20). The greatest amount of variability exists in total relative dry matter. The greatest difference in the coefficients of variation between environments occurs in top relative dry matter. However, this character exhibits a smaller range than does total relative dry matter.

With respect to number of branches the 27 white spruce sources had coefficients of variation of 20.4% and 23.8% respectively, in the northern and southern environment (Table 20). Thus, numbers of branches appear to have greater standard deviations relative to their means than do total and top relative dry matter. Although these different variables were measured in different ways, it appears that greater variability exists among the white spruce sources for number of branches than for total or top relative dry matter.

CHARACTER	STANDARD DEVIATION	MEAN	COEFFICIENT OF VARIATION	ENVIRONMENT
TOTAL RELATIVE	0.025	0.312	0.080	NORTHERN
DRY MATTER	0.021	0.278	0.075	SOUTHERN
TOP RELATIVE	0.021	0.362	0.058	NORTHERN
DRY MATTER	0.024	0.364	0.065	SOUTHERN
NUMBER OF	1.674	8.170	0.204	NORTHERN
BRANCHES	2.333	9.762	0.238	SOUTHERN

Table 20. Coefficients of variation for total and top relative dry matter and number of branches in two environments using source means for 27 white spruce per environment.

IV. Discussion

Validity of Null Hypotheses

It is evident from the data that statistically significant differences among Alberta sources of white spruce exist with respect to some measured characters. Thus, the first null hypothesis of this experiment must be rejected. Those characters exhibiting significant differences are total relative dry matter, top relative dry matter and number of branches. These significant differences occur among sources within both environments. Assuming that phenotypic expression is equivalent to genotypic expression (under constant environmental conditions), it follows that the significant populaticn differences shown are genetic in nature. Thus, the second null hypothesis must also be rejected.

With respect to discernible patterns of variability, correlation analysis and Duncan's Multiple Range Tests have indicated that definite patterns do exist, and that these patterns are related to environmental parameters. Thus, the third null hypothesis is rejected.

Top and Total Relative Dry Matter

Relative dry matter or the measure of dry weight relative to fresh weight and its use as a diagnostic measure in diversity studies of forest tree species was pioneered by

Olof Langlet in the late 1920's and early 1930's (Langlet 1959, 1967). Langlet (1967) used the term "dry matter percentage" to denote the ratio of dry weight to fresh weight. In this study "dry matter percentage" is equal to relative dry matter x 100. Langlet's (1967) investigations of Scots pine (*Pinus sylvesteris* L.) and Norway spruce (*Picea abies* (L.) Karst) provenances "demonstrated that the dry matter percentage in seedlings during the late autumn exhibits a remarkably strong correlation with the length of growing season of the particular habitat ...." Specifically, Langlet found that length of the growing season and latitude were the only significant environmental parameters related to the pattern of dry matter variation.

In this study, as has been previously mentioned, total and top relative dry matter were found to be good diagnostic measures in the investigation of genetic variability in white spruce in Alberta. Correlation analysis indicated that, with the exception of total relative dry matter in the northern environment, dry matter tended to increase as latitude of the source increased. This trend was prevalent in both environments. It should be noted that correlations for both total and top relative dry matter with respect to latitude for the eastern transect sources in the southern environment (sources 1 through 8) were highly significant ($r=0.782$ and $r=0.808$ respectively). In general the relationships in the southern environment were more significant than the same relationships in the northern

environment.

The pattern of variation of total and top relative dry matter were similar in both environments. Relative dry matter of all sources tended to decrease with increasing elevation. The plants in the southern environment again tended to have more significant relationships with elevation than those in the northern environment.

The elevational relationship mentioned above appears to contradict the latitudinal relationship previously discussed. One would logically assume that higher elevation sites would be climatically similar to higher latitude sites. Thus the trends with respect to latitude and elevation should generally parallel each other. However, this was not shown here. One possible explanation for the apparent anomaly is that the photoperiodic change caused by displacement in latitude may be much more influential than displacements in elevation when considering relative dry matter production. This, together with the fact that there is a very strong inverse relationship between latitude and elevation of the sources used in this study ($r=-0.871$, $P \leq 0.001$), would lead one to believe that the elevational trends probably confirm the strong influence of latitude of the source on relative dry matter.

It has been pointed out by Wiersma (1964) that converted latitudes (ie. latitudes adjusted for differences in elevation) can often be used to clarify the relationship

between measured characters and latitude and elevation of sources in provenance tests. For that reason converted latitudes were employed in this study. Wiersma assumed from investigation of Langlet's work with Scots pine and Norway spruce in Sweden that an adjustment of 1°N. latitude for 100m. increase in elevation was appropriate. Thus, using a base elevation of 2000 ft. or 606.1 m. the converted latitude formula used in this study was:

$$CLAT = ((ELEV.-606.1)/100) + LAT.$$

In correlation analysis, with the exception of top dry matter in the southern environment, relative dry matter tended to decrease with increased converted latitude. Visually, these relationships (Figures 7, 8 and 13) show that, in general, high elevation, southern sources (ie. those with high converted latitudes) have less autumnal relative dry matter than northern, low elevation sources (ie. those with low converted latitudes). Thus, it is again evident that in terms of autumnal relative dry matter, northern sources tended to out-perform southern sources in both environments.

The preceding discussion can be further emphasized by the results of the Duncan's Multiple Range Test. The source maps of significantly different populations in both treatments (Figures 18 through 21) show that, in all but one case (total relative dry matter in the northern environment), northern sources have significantly higher total and top relative dry matter than do southern sources.

The exceptional case, total relative dry matter in the northern environment, indicates that a number of northeastern sources and two extreme southern sources have significantly higher relative dry matter than any of the other sources.

The rankings of sources used in Duncan's Multiple Range Test allows one to determine:

1. how sources are reacting, with respect to a given character, to the different test environments,

2. if any sources are maintaining exceptionally high or low levels of performance, with respect to a given character, in both environments.

In general, considering only total relative dry matter rankings, those sources that performed best in the northern environment did relatively poorly in the southern environment. Only three sources (numbers 8, 21 and 22) of the top ten in the northern environment remained in the top ten in the southern environment. Of these only one (source 8) remained in the group with the significantly highest total relative dry matter values. With respect to top relative dry matter, those sources which performed best in the northern environment tended to perform poorer in the southern environment. However, this change in performance was not nearly as evident as it was in the total relative

dry matter measures. Five of the top ten sources (numbers 8, 22, 24, 25, and 27) from the northern environment remained in the top ten in the southern environment. Of these, four sources (numbers 8, 24, 25 and 27) remained in the group with the significantly highest top relative dry matter.

The poor performers with respect to both total and top relative dry matter in both environments were high elevation, east-slope sources (numbers 10H 13H, 16M, 16H). These sources remained in the bottom ten in all cases.

Number of Branches

Differences in number of branches tended not to be as significant as total or top relative dry matter. The pattern of variability of number of branches with respect to environmental variables was also not as well defined as it was with total and top relative dry matter. Specifically, when considering all sources, number of branches only showed a significant correlation in the southern environment with respect to converted latitudes. It should be noted, however, that in both environments there were significant correlations of eastern transect sources with respect to latitude. There was also a significant correlation between number of branches of northwestern sources and latitude of the source, in the southern environment. Thus, it appears evident that a weak but noticeable trend exists for number of branches to decrease as latitude of the source increases,

particularly under simulated southern Alberta conditions.

The pattern of variability with respect to number of branches and latitude can be further illustrated by the results of the Duncan's Multiple Range Test. Source maps of significantly different groups of sources from either environment (Figures 22, 23) indicated that a band in the central and north-central region of the province tended to have significantly higher numbers of branches than sources to the north or south of this area. This band includes more sources and specifically more northern sources under southern environmental conditions than under northern environmental conditions.

In terms of rankings it appears that in general sources that perform well under northern environmental conditions (i.e. those with high numbers of branches) perform as well or better under southern environmental conditions. Six of the top ten sources under northern environmental conditions (sources 1, 2, 3, 5, 15, and 19) remained in the top ten in the southern environment. However, only two sources (sources 1 and 15) remained in the group with a significantly greater number of branches. Both northern and southern sources (i.e. sources 8, 10, 12, and 21) were poor performers in both environments.

Comparisons With Other Known Patterns of Variation

As has been previously mentioned, Langlet (1959, 1967)

has shown that dry matter percentage of Scots pine tended to be closely related to latitude of the source (ie. dry matter percentage increased as latitude increased). He stated that "dry matter substance" could be "used as a measure of the degree of autumnal hardiness (Langlet 1967)." Furthermore, he found that "evolution of hardiness among pine seedlings during the autumn is solely dependent on the inherited adaptation to the length of the season of vegetation and to the latitude - which in turn denotes length of daytime or darkness (Langlet 1967)." The data from the present study appear to agree with this latitudinal relationship. However, Langlet also indicated that northern and southern provenances of Scots pine on "warm climate sites" appeared to produce the same dry matter percentage. Under colder site conditions southern provenances did not perform as well as northern provenances, and did not do as well as they did in their original habitats. The present study indicates that white spruce does not appear to operate like Scots pine. Northern sources of white spruce had greater relative dry matter than southern sources in both northern and southern environments. As Langlet (1967) pointed out in comparing Scots pine and Norway spruce, even species with coincident ranges tend to show different patterns of geographic variability. Thus, it is not odd that the pattern of variability exhibited by the Alberta sources of white spruce tends to differ from that of Scots pine in Sweden.

As mentioned earlier, clinal variation related to

latitude of the source was evident in the range-wide white spruce provenance studies. In fact, Wright (1976) indicated that clinal variation is strongly correlated with latitude in the boreal forest. Relative dry matter measures for Alberta sources of white spruce exhibit a similar clinal pattern of variation.

The pattern of variation exhibited by white spruce for number of branches does not appear to have the same relationship with latitude of the source as does relative dry matter. Although there appears to be a weak tendency for number of branches to decrease as one moves from the central portion of the province northward, the more significant relationship appears to be the greater number of branches exhibited by sources in the central and north-central region of the province relative to all others tested. This band of "high branch number sources" appears to be similar to the zone found by Hellum (1971) for seed weight of a number of Alberta sources of white spruce. Hellum's "central zone" extended from 53° to 57°N latitude. In the present study the "central zone" extends from about 53° to 58°N latitude.

V. Conclusions and Implications

The preceding discussion indicates that:

1. there is genetic variability in total and top relative dry matter and number of branches in white spruce in Alberta,
2. total and top relative dry matter show significant relationships with latitude of the source. Northern sources show significantly higher dry matter production than southern sources in both northern and southern environments,
3. there is a band of sources with large numbers of branches in the central and north-central part of Alberta,
4. sources 8, 24, 25 and 27 showed consistently high total and top relative dry matter production in both environments. High elevation, east-slope sources (i.e. sources 10H, 13H, 16M and 16H) had consistently low relative dry matter production in both environments,
5. sources 1 and 16L had significantly greater numbers of branches in both environments,
6. coefficients of variation for total and top relative dry matter ranged from 5.8% to 8.0% over different environments,
7. coefficients of variation for number of branches ranged from 20.4% to 23.8% over the different environments.

If one can assume, as Langlet (1967) has, that autumnal relative dry matter essentially measures winter hardiness, it appears that the northern Alberta sources of white spruce are significantly more hardy when grown in both simulated northern and southern Alberta environments. In addition, high elevation, east-slope sources appear to be much less hardy than any of the other sources tested.

The hardiness of northern sources may well be explained by the strong relationship between relative dry matter and latitude of the source. As one changes latitude of the source, one of the major environmental parameters that also changes is photoperiod. Lavee (1973) hypothesized that photoperiod is the most important environmental trigger involved in the initiation of dormancy. The initiation of dormancy as well as the increase in dry matter accumulation are two of a number of processes involved in a plant's preparation for winter. If photoperiod is a major trigger in these processes, northern sources, which have adapted to the longer days of the northern growing season, when grown in a southern environment will receive their photoperiodic trigger to harden-off early in the southern growing season. Thus, northern sources should have greater relative dry matter accumulation than the southern sources by autumn. Conversely, when southern sources are grown in a northern environment, they will not receive their relatively short photoperiod trigger until very late in the northern growing season. Again, northern sources should have accumulated more

dry matter than the southern sources by the end of the growing season. Thus, in both environments northern sources would be expected to have greater relative dry matter than southern sources.

The low production of relative dry matter and associated poor winter hardiness of the high elevation, east-slope sources may be explained by a different set of selective forces at work at these high elevations compared to elsewhere in the province. These sites tend to have a greater degree of non-standard environmental conditions. Severe drought conditions during the growing season, stress due to exposure, poorly developed soils (i.e. thin soils on rocky parent material), and the occurrence of warm temperatures for short periods during winter (caused by chinooks, inversions, etc.) prevail on these higher elevation sites. It is likely that these factors, as selective forces, have had a greater influence on the survival of white spruce at higher elevations than has winter hardiness. Thus, with less emphasis on winter hardiness these sources could be expected to exhibit lower relative dry matter.

The pattern of variation in number of branches is not similar to that of total or top relative dry matter and does not show similar, significant relationships with environmental parameters. However, the banding pattern in number of branches (i.e. greater number of branches from

sources in the central and north-central region of the province) appears similar to the pattern of variation in seed weight which Hellum (1971) illustrated. Possibly, the selective forces which have acted to shape the pattern of variation for seed weight may be similar to those which shaped the pattern of variation for number of branches.

It has been postulated that grassland expanded into the former forests of central and north-central Alberta approximately 5000 to 8000 years ago (Hansen 1949, 1952; Moss 1952, 1955). During this period, termed the Hypsithermal Interval (Deevey and Flint 1967), the climate was becoming warmer and drier (Ritchie 1976). Moss (1952) has postulated that extensive grassland expansion occured at this time. This expansion was so extensive that it could have connected the Peace River region with the parkland of south-central Alberta. Lichti-Federovich (1970) and Raup (1934, 1935) have postulated that grassland species may have increased in relative abundance during this period, but that extension of grassland species into the Peace River region cannot be conclusively proven. In either case, it appears that during the late post-glacial period in Alberta a warming and drying trend cccurred with the result that the boreal species may have been either partially or totally eliminated from central and north-central Alberta and only persisted in the cooler and moister east-slope and northern regions of the province.

Separation of these two boreal zones may have continued for 2000 to 3000 years (10 to 60 generations of white spruce). This isolation, combined with the probable genetic differentiation occuring in different environments, may have resulted in two genetically distinct groups of white spruce in Alberta near the end of the Hypsithermal Interval. During the decline of the Hypsithermal Interval, as the climate became cooler and moister, the boreal species appear to have begun to encroach and reestablish themselves on the extended grassland region. Thus, the region may have been a zone of genetic mixing between the two previously isolated groups of white spruce.

Selective forces acting on white spruce during the period of reestablishment would tend to favor different characteristics than those favored under the more normal late-successional situation. Lighter spruce seed would disperse farther, and thus would become established more quickly at greater distances, than would heavy seed. Thus, lighter seed would tend to have a competitive advantage in the reestablishment of the grassland region due to the fact that they would be the first seeds on the sites.

The relatively open sites which would likely have been prevalent in the region of reestablishment during the post-Hypsithermal period would favor individuals with more branches and fuller crowns. Those plants able to produce more branches and develop fuller crowns would be more

photosynthetically efficient and as such would have a selective advantage over less photosynthetically efficient plants. Selection during the period of reestablishment then might have favored white spruce with lighter seed and greater number of branches than those elsewhere in the province.

In the case of complete isolation, genetic mixing and differentiation due to the selective forces at work in the region of reestablishment would lead to significant genetic differences among sources from this region compared with those from elsewhere in the province. In the case of incomplete isolation, gene flow would be restricted but not nonexistent. Genetic differentiation during the Hypsithermal Interval would not have been as significant as in the previous case. Thus, upon reestablishment of the grassland region, little if any genetic mixing may have occurred. However, the selective forces at work in the grassland would remain the same as in the first case. Thus, although no genetic mixing may have occurred, genetic differentiation could still have been feasible during the period of reestablishment. In both cases sources from the central and north-central portions of Alberta could be expected to show significant genetic differences from sources elsewhere in the province, particularly with respect to number of branches and seed weight.

This may explain the pattern of variation of seed

weight and number of branches for white spruce in Alberta. However, this hypothesis does not explain the pattern of variation in total and top relative dry matter. These characters exhibit continuous variation and give no evidence of the region of spruce retreat and reestablishment. It may be possible that during the separation (complete or incomplete) of the boreal zones, selection for frost hardiness in white spruce through relative dry matter continued in the two groups. It is also quite feasible that during and since the post-Hypsithermal period this same selective force continued to be in effect. If this is true, then the outcome would likely have been a continuous pattern of variation in relative dry matter. Thus, it may have been possible for a variety of selective forces, acting on a number of characters, to shape the differing patterns of variation illustrated in this study.

Implications

There are several implications of the present study:

1. Movement of seed within the province:
   a. assuming the major criterion for survival on planting sites is winter hardiness, northern sources of white spruce can be moved and will survive throughout the province (with the exception of movement to high elevation, east-slope sites),
   b. local sources should be used on high elevation,

east-slope sites. These sources should not be moved elsewhere due to poor winter-hardiness,

c. central and north-central sources will have more branches particularly on southern Alberta sites.

2. Tree improvement:

a. sources that are the most winter hardy may not grow the best. It may be necessary to establish a number of detailed provenance and progeny tests on a wide variety of sites to adequately determine those sources or families which will provide the best hardiness and the best merchantible characters,

b. movement of northern sources south may not be wise due to their possible inability to make maximum use of the southern growing season. Thus, although these sources may survive well in southern environments they should be excluded from any breeding program intended for southern sites,

c. since the northern sources could feasibly be moved freely in the northern portion of Alberta, intensive provenance and progeny testing on a wide variety of sites may be useful in determining the best sources and families for reforestation of northern Alberta sites.

d. within the above constraints it would be premature to establish specific seed collection and planting zones for white spruce in Alberta.

VI Recommendations For Further Research

This study has attempted to elucidate some aspects of the genetic variability of white spruce in Alberta. Several questions as to patterns of variability and characters indicating significant genetic variation have been answered. However, this investigation has given only a partial view of the total picture of genetic variability of white spruce in Alberta. Many questions remain unanswered and require further research. Some major ones are:

1. the present study was unable to accurately determine among-family variation within seed sources and was limited in the amount of site data that could be collected for each source. Thus, it would be useful to initiate a study similar to the present study, using hand picked seed from known mother trees. In this way one could analyze within-and among-family variation as well as within-and among-source variation. By having exact locations of sources one would be able to measure more site data. Thus, the possibility may exist for more accurate analysis of relationships between measured characters and environmental parameters of the source. This same study could be utilized in field tests. In this case one would be better able to analyze variation under field planting conditions which cannot be fully simulated in the laboratory,
2. this study did not investigate variation in dormancy

and bud initiation. However our own study results indicate that winter hardiness may be a major selective force influencing white spruce in Alberta. Thus, it would be useful to initiate a controlled environment study, similar in design to that in the first recommendation, to investigate variation in bud burst, dormancy, and their relationship to total and top relative dry matter variation as well as to environmental parameters of the source,

3. this study was unable shed light on long term character development in white spruce. Although there were evident patterns of variation, it should be kept in mind that these are based on two-year old seedlings. White spruce has a life span ranging from 80 to 400 years. Thus, it would be useful to establish long-term progeny tests under field conditions using a collection design similar to that in the first recommendation. In this way parent/progeny correlations for a number of characters could be studied, source and family performance in merchantable and non-merchantable characters in the long term could be established, and factors influencing source or family performance with respect to a given character could be investigated.

Summary

27 sources of white spruce were used to investigate the nature and amount of genetic variability of white spruce in Alberta. Seedlings from these sources were grown in containers for two growing seasons, in a factorial design, under two controlled environment regimes simulating northern and southern Alberta forest conditions. Height growth was measured at bi-weekly intervals throughout both growing seasons. At the end of the experiment height, diameter, number of branches, total and top fresh weight, total and top dry weight, fresh and dry weight root/shoot ratios, and total and top relative dry matter were measured.

Analysis of variance was used to determine the significance of differences among sources. The relationships of characters with environmental parameters of the source were tested using regression analysis. Duncan's Multiple Range Test was used to determine significantly different groups of sources. Principle components analysis was employed, using all characters, to determine significant multivariate source groupings.

Analysis of variance indicated that total and top relative dry matter and number of branches were the only characters with significant among-source variation. Regression analysis and Duncan's Multiple Range Test showed northern Alberta sources to have significantly higher total and top relative dry matter than all other sources, while

sources from central and north-central Alberta were shown to have significantly greater branchiness than all other sources tested. Assuming relative dry matter to be a measure of winter hardiness, the northern Alberta sources were the most hardy and the high elevation, east slope sources the least hardy of all sources tested.

The patterns of variability of relative dry matter and number of branches differed. Relative dry matter exhibited continuous variation with respect to latitude and elevation of the source, similar to that in a number of characters tested previously in range-wide studies of white spruce. Number of branches exhibited a banded pattern of variation, which appeared to be similar to that previously reported for seed weight of a number of sources of Alberta white spruce.

It appears feasible that the patterns of variability reported in this study could have developed since the late post-glacial period in Alberta. This period may have been characterized by the retreat and reestablishment of boreal species from central and north-central Alberta due to the extension and retreat of grasslands in this region. The effects of isolation as well as selection and genetic differentiation over a period of several thousand years may have resulted in the differing patterns of variation illustrated in this study.

The results of this study indicate that:

1. Northern Alberta sources of white spruce can be moved

and will survive throughout the province (with the exception of movement to high elevation, east-slope sources).

2. Local sources should not be moved from high elevation, east-slope sites.
3. Central and north-central sources will have more branches particularly on southern Alberta sites.

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Appendix A

Growth Chamber Specifications

Conviron Model E7 and E8M

Light Intensity	0 to 10000 lux (E8M) 0 to 25000 lux (E7) (Seedlings maintained at 10000 lux at seedling level throughout experiment).
Photoperiod	24 hour trip-switch timers
Day-Night Temperatures	10°C to 45°C (lights on) ± 0.5°C 4°C to 45°C (lights off) ± 0.5°C (temperature regulated as per Appendix B).
Relative Humidity	0 to 100% ± 3% (Wet Bulb - Dry Bulb Differential control using a centrifugal atomizing humidifier) (Humidity regulated as per Appendix B).

Warren/Scherer Model Cel 4-4

Light Intensity	0 to 15000 lux (maintained at 10000 lux during experiment).
Photoperiod	24 hour trip-switch timer.
Day-Night Temperature	10°C to 43°C (lights on) ± 0.5°C 5°C to 43°C (lights off) ± 0.5°C (temperature regulated as per Appendix B).
Relative Humidity	40 to 100% ± 3% (Wet Bulb - Dry Bulb Differential control using a centrifugal atomizing humidifier) (Humidity regulated as per Appendix B).

Appendix B

Growth Regimes

A. First Season: Conviron E8M and Warren/Scherer Cel 4-4 (environments reprogrammed and rotated on a two week interval)

Date	Northern Environment R.H. 56% Photoperiod (hr)	Temp. (°C) Day	Night	Southern Environment R.H. 50% Photoperiod (hr)	Temp. (°C) Day	Night
Feb. 2/77	19.5	21.7	7.6	17.0	18.2	4
Feb. 16	19.0	23.2	9.0	17.25	19.7	5.8
Mar. 1	18.0	22	8.2	17.25	22.6	7.2
Mar. 15	16.75	21	7.3	17.0	25.2	8.5
Mar. 29	15.25	19.8	5.0	16.25	24.4	7.8
Apr. 12	12	13.3	4.0	15.50	23.7	7.0
Apr. 26				14.50	21.1	5.4
May 10				13.50	18.5	4.0
May 24				12.0	13.0	4.0

Appendix B (cont.)

B. Second Season: Conviron E7
(environments reprogrammed and rotated on a two week interval)

Date	Northern Environment R.H. 50% Photoperiod (hr)	Temp. (°C) Day	Night	Southern Environment R.H. 50% Photoperiod (hr)	Temp. (°C) Day	Night
Jul. 5/76	18.2	13.5	4.0			
Jul. 19	19.25	16.8	4.0			
Aug. 2	19.5	20.0	6.2			
Aug. 16	19.5	21.5	7.8	15.7	13.0	4.0
Aug. 30	19.0	22.8	9.2	16.4	16.0	4.0
Sept. 13	18.0	21.8	8.4	17.0	17.8	4.0
Sept. 27	16.75	21.0	7.6	17.25	19.5	5.6
Oct. 11	15.25	17.0	5.0	17.25	22.6	6.6
Oct. 25	14.0	13.0	4.0	17.0	25.8	7.5
Nov. 8	12.0	8.0	4.0	16.25	24.8	7.2
Nov. 22				15.5	23.9	7.0
Dec. 6				14.5	21.4	5.0
Dec. 20				13.5	19.0	4.0
Jan. 3/77				13.75	16.0	4.0